

The effects of testosterone on embodiment: Implications for social power

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Abstract

Following recent trends in the neurosciences in which the body is seen as a constituting factor in mental experience and behavior, this thesis examined the role of testosterone in mapping the state of the body. The general aim was thus to contribute to the literature on the embodied basis of power by asking whether a change in the neurochemistry associated with social power has any effect on embodiment? Accordingly, in a series of randomized, double-blind, placebo controlled studies, this thesis assessed for the first time the effects of a 0.5mg dosage of testosterone on three important dimensions of embodiment in samples of women: 1) The perception of internal physiological signals (interoception), 2) Body ownership, and 3) The experience of sensory-motor agency. Psychological tests measuring emotion and personality were integrated into the design. Using a heartbeat tracking task, testosterone was shown to increase interoceptive accuracy at baseline, but this advantage was lost following ostracism in an online ball tossing game. In experiment two, it was found that testosterone compared to placebo prevented a decline in limb temperature during the Rubber Hand Illusion, a commonly used paradigm for manipulating experiences of body ownership and for measuring homeostatic changes related to disembodiment. In experiment three, testosterone was found to increase the implicit sense of agency as measured in terms of intentional binding, a task which exploits the tendency to perceive a contraction in time when one's own actions are felt to be casually related to external effects. Results indicate that testosterone has the capacity to improve interoceptive accuracy, is able to help regulate homeostasis in response to erroneous top-down beliefs about the body, and to increase the feeling of sensorimotor control. While the limitations of this data are acknowledged, these main findings suggest that testosterone is able to modulate the experience and representation of the body and offer insight into some of the rudimentary embodied mechanisms via which the hormone might support the rise to power.

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This article forms part of Chapter 4.

Statement of contribution:

I, Donné Minné née van der Westhuizen, was responsible for the conceptualisation of the study, the literature search and review, data collection and statistical analyses, interpretation of the findings and the write-up.

Chapter 1| Introduction

1. Introduction

“What is more important for us, at an elemental level, than the control, the owning and the operation, of our own physical selves?” – Oliver Sacks, 1985.

Many years before the field of embodied cognition gained eminence in the neurosciences, the celebrated neurologist, Oliver Sacks, in his account of a patient who lost her sense of the body (Sacks, 1987), brought attention to the importance of corporeality in emotional and mental life. The body, in his words, “is beyond question,” it is “elemental”. But what exactly should we understand to be the “elemental level”? Sacks describes the unimaginable “nothingness” of his patient and goes on to quote Wittgenstein. He says, “This unquestionability of the body, its certainty, is, for Wittgenstein the start and basis of all knowledge and certainty” (p.127).

For Sacks – and Wittgenstein – our most rudimentary sense of stability and “direction” in the world – those elemental feelings that hold our mental lives *together* – emerges from control and ownership of the body. In this thesis, I will extend this key idea and begin to ask whether what we take, essentially, to be *power*, that implicit drive for agency and fundamental capacity to act and to influence (Overbeck & Park, 2001; Russel, 1938), is a basic property inherent to the owning and control of a body. Individual differences in embodiment might in turn explain and describe some of the individual differences in power. This hypothesis is premised on the idea that power, like other social-emotional states, might manifest firstly in the physical, bodily domain but then extend to the conceptual as information is registered in the more basic regions of the brain and begins to associate hierarchically (Critchley & Garfinkel, 2018; Maister, Slater, Sanchez-Vives & Tsakiris, 2015).

I will begin with a general overview of power and how it manifests in the social sphere before focusing specifically on the hormone, testosterone, considered to be a core neurochemical substrate of power and dominance (Eisenegger, Haushofer & Fehr, 2011; van der Westhuizen & Solms, 2015). This review will highlight some of the conceptual and

methodological challenges in the existing literature, which call most notably for a unifying paradigm that is able to bring coherence to cross-cultural research on testosterone and social behaviour. This unifying paradigm, I argue, is embodied cognition. A number of findings to date within this field already highlight the important ways in which power might be embodied. We have seen, for example, that socially powerful individuals are more accurate in perceiving their internal bodily signals (Moeini-Jazani, Knoeberle, de Molière, Gatti & Warlop, 2017), that malleable bodily representations are linked to conformity behaviour (Paladino, Mazzurega, Pavani & Schubert, 2010) and that feeling disempowered leads to a disruption in the processing of implicit action-effect relationships (Obhi, Swiderski & Brubacher, 2012). The purpose of this thesis is therefore to extend these findings and investigate the effects of a single, 0.5mg dosage of testosterone on three well-known aspects of embodiment: Interoceptive awareness, body ownership and the sense of agency. This is a necessary first step toward describing the hormonal regulation of embodiment and its potential role in the phenomenology and emergence of social power.

1.1 The Psychology of Power

Power has fascinated society since the beginning of time. It is a ubiquitous phenomenon which has shaped the contours of our collective recorded histories. Highly coveted for its intimate association with freedom, power is also feared by those without it. Not surprisingly then, the concept of power is a reoccurring theme in literature (Adler, 1927/2009; Fehr, Herz & Wilkening, 2013; Foucault, 1979; Guinote, 2010; 2017; Keltner, Gruenfeld & Anderson, 2003; Rucker & Galinsky, 2008; Russell, 1938; Nietzsche, 1901; Webber, 1947/1964). Consequently, definitions of power abound. Deriving from the Latin word, *potere*, power means “to be able” and such agency in powerful individuals is seen to be deployed with a sense of entitlement (Kipnis, 1972) and a desire to exert control (Fiske, 1993). Though power is often seen to reside within the individual, it is nonetheless a relational concept and is dependent on the relinquishment of power from other individuals – from other acting bodies. As such, several authors (Overbeck & Park, 2001; Sturm & Antonakis, 2015) define power as the ability and means to asymmetrically enforce one’s will over other social entities. Having power is thus about acting voluntarily in desired ways. In the social domain where every interaction *always* involves a negotiation of interests, this agency necessarily becomes an issue of control even when social control itself is not the primary objective.

1.1.1. Power as ‘wants and desires’, amplified and unimpeded.

In a comprehensive review of the literature, Guinote (2017) motivates for a more complex explanation of power and argues that powerful individuals tend to achieve control because of a triad of traits she refers to as *activation*, *wanting* and *seeking*. Power is framed here as a property of having *strong agendas* and being *action-impelled*, which tends to come at the expense of others’ needs. From this perspective, power is not simply a downstream, somewhat incidental consequence of the brain’s general appetitive system (Panksepp & Biven, 2012), which is seen by some to override those of others in the race for valuable goods (Berdahl & Martorana, 2006; Keltner, Gruenfeld & Anderson, 2003; Langner & Keltner, 2008). Instead, in Guinote’s framework, the intensification of goal-directedness lies at the heart of what it means to be powerful.

For instance, empirical studies have shown that powerful individuals are confident (Briñol et al., 2007; Fast et al., 2012) with higher levels of self-esteem (Hofstede et al., 2002; Wojciszke & Struzynska-Kujalowicz, 2007) and they pursue their goals with more perseverance and persistence (Guinote, 2007). Particularly under pressure, power is linked to improved performance (Kang et al., 2015). Powerful individuals tend to express their desires and wishes more opening and directly (Guinote, Judd & Brauer, 2002) and rely more strongly on “gut feelings” (Dane & Pratt, 2007). In this way, core values and dispositions are chronically accessible and magnify the “active self” (Galinsky, Gruenfeld & Magee, 2003; Guinote & Chen, 2016). Goal pursuit among the powerful is characterized by enhanced focus, certainty and singlemindedness (Guinote, 2007b; Smith & Trope, 2006). This is seen in rapid decision-making, less delay in initiating a response (Magee, Galinsky & Gruenfeld, 2007) and stronger reactions to violations of “unfair” treatment (Sawaoka et al., 2015). Powerholders often report the feeling of being in control (Scholl & Sassenberg, 2014), display increased verbal output (Hall, Coats & LeBeau 2005) and tend to be successful in persuading others to adopt their own goals (Laurin et al., 2016) while resisting others’ wishes (Galinsky et al., 2008). One mechanism in this regard is reduced attention toward cues signalling the emotional demands of others (Fiske, 1993; Goodwin, Gubin, Fiske & Yzerbyt, 2000). Instead, Overbeck and Droutman (2013) have argued that socially powerful people use the self as a heuristic for inferring the internal states of others, i.e. “self-anchoring”.

The inherently dynamic nature of social hierarchies means that even in times of relative stability, ongoing power plays may be necessary but also so subtle as to go unnoticed. For instance, an established leader might simply charm their followers (Den Hartog & Verburg, 1997). Also, powerful individuals might act in unconscious ways to implicitly attract greater social attention – a highly coveted reward – from lower ranking members and be perceived by them as more competent than they actually are (Anderson & Kilduff, 2009). From this perspective, power dynamics pervade almost all aspects of interpersonal interaction.

1.1.2 Summary: Power, the self and self-regulation.

To sum, power emerges when goal-pursuit is amplified to the extent of being unimpeded. In the behavioural literature, this type of motivation tends to be referred to more simply as an “approach orientation” (Terburg & van Honk, 2013). In the social domain where other’s wishes stand as impediments, the capacity for power itself appears to drive much of the imperative to then exert control. This instatement of control can be framed in the same way as other attempts to manage overwhelming impulses, that is, as an emotion regulation strategy (Declerck, Boone & Brabander, 2006). Thus, in a more nuanced account of power, efforts to take control could be regarded as the expression of *self-regulation*. Endowed with generous ability to sense motivation and initiate action in the pursuit of an upwelling of intention, the potential energy must find discharge in the social sphere. This view is echoed by Russel’s (1938) well-known analogy that power in the social sciences can be likened to energy in the physical sciences. Framing power as being driven fundamentally by capacity urges us to ask how this capacity arises and where it comes from?

1.2. Neuroanatomy of power

As a start, a cross-species approach (Panksepp & Biven, 2012) is well suited to answering these sorts of questions where invasive experimental manipulations, not always possible in human research, are able to reveal key brain mechanisms supporting power. Studies using immunocytochemistry and artificial stimulation have identified a common set of neural structures underpinning the expression of power across different species, outlined by the high density of testosterone and vasopressin (AVP) receptors surrounding the anterior hypothalamus (for review see van der Westhuizen & Solms, 2015a). Other regions include the medial amygdala, bed nucleus of the stria terminalis, lateral septum and the periaqueductal

gray (PAG; Albert et al., 1992; Bamshad & Albers, 1996; Ferris, 1992; Koolhaas, van der Brink, Roozendaal, & Boorsma, 1990; Kruk et al., 1983; Pan, Xu, Young, Wang, & Zhang, 2010; Rosen et al., 2006). Behaviours activated by this neural circuit establish rank and usually involve initial physical fighting followed by intimidation displays and defensive scent-marking to secure territory. Often, these behavioural patterns represent attempts to increase perceived body size and consist of changes in posture or movement (Goodall, 1986; Mazure, 1985; Piaskowski, Weise & Sigler Ficken, 1991).

The subcortical structures underpinning the expression of power form part of the limbic system and are in keeping with a primary emotion account of dominance motivation (Panksepp & Biven, 2012). However, while many studies provide unequivocal support for the elicitation of dominance behaviours from direct stimulation of subcortical sites, the heterogeneity of neural control and overlap with other basic emotion circuitries makes the identification of a consistently recognizable subcortical circuit across species difficult (van der Westhuizen & Solms, 2015a). It is unclear how exactly the coherence in the drive for power emerges.

More conclusively, a recent seminal study in rats showed that dominance in competition was reliably achieved not as a function of social aggression or physical strength, but by the initiation and maintenance of more effortful behaviours sustained by the dorsal medial pre-frontal cortex (dmPFC) (Zhou et al., 2017). These findings are consistent with earlier research showing that molecular manipulations that increase or decrease synaptic efficacy in neurons of the dmPFC cause a corresponding elevation or descent in social rank, respectively (Wang, Zhu, Zhu, Zhang, et al., 2011). In human subjects, activation of dmPFC has been linked to *self*-reference while the ventral aspect is more closely related to *other*-related references (Denny, Kober, Wager & Ochsner, 2012). The dmPFC has also been implicated in cost/benefit analyses and effort-based decision-making, leading Zhou et al. (2017) to conclude that this region may underpin perseverance and the expression of dominance drive in competition.

This account of dominance in social hierarchies aligns more closely with human studies of power and also animal work that indicates that competitive aggression is characterized predominantly by only superficial wounding (Litvin, Blanchard, Pentkowski, & Blanchard, 2007). What appears to be attempts at simply inflicting harm during competitive social

interactions may instead be regarded as a form of assertiveness. Circuitry within the medial PFC may be involved in this type of resilience. Maier et al., (2006) demonstrate that the detection of *degree of control* is instantiated by the mPFC. For instance, experimental studies in rats have shown that the experience of uncontrollable stress, which leads to a submissive phenotype, is mitigated by activation of the vmPFC, analogous to an “illusion of control”. Most critically for approach-oriented behaviour, an initial experience of controllability over a stressor appears to alter the vmPFC response to successive stressors, such that it activates even in situations where the subsequent stressor cannot be controlled. Changes in the connectivity between limbic and cortical brain regions may thus account for the regulation of power in social interactions (Mehta & Beer, 2010; Schutter & van Honk, 2004; van Wingen, Mattern, Verkes, Buitelaar et al., 2010).

Thus, to conclude, across species, power is closely linked to effort and control in relation to self and others. The term, “territoriality”, is well suited to describe this quality of emotion where activation of effort-regulating brain regions may occur in response to alleged intrusions to the perceived boundaries of owned ‘spaces’, and this may extend conceptually to occupied places in the social hierarchy. Many studies have accrued to date showing that behaviours recruited in the service of maintaining control appear to be tightly linked to the activity of the steroid hormone, testosterone. The following section will provide an overview of the role of testosterone in power and emotion.

1.3. The role of testosterone in power

Although the neurochemical profile of power and dominance is heterogeneous to some extent (van der Westhuizen & Solms, 2015a) many studies have demonstrated a critical role for testosterone in the rise to power. Testosterone is considered a male-type sex steroid hormone. Indeed, aside from its well-known role in masculinization, it is known to support a variety of bodily processes that enhance physical performance, such as stamina, strength, bone mass and of course, male virility (Sinervo, Miles, Frankino, Klukowski et al., 2000; Sinneasael, Boonen, Claessens, Gielen et al., 2011; Wang, Swerdloff, Iranmanesh, Dobs et al., 2013). The Leydig cells of the testes are the primary site of production in men, while in females, testosterone is produced in the ovaries and adrenal glands (Mazur & Both, 1998). Males have roughly 10 times the amount of circulating testosterone than females, although females tend to be more sensitive to the hormone (Durdiakova, Ostannikova, Celec, 2011).

Closely implicated in dominance behaviour, is AVP. Testosterone is known to sustain the expression of AVP, a peptide hormone referred in other contexts as antidiuretic hormone because it regulates water retention. Studies have found significantly higher concentrations of AVP in male brains (Caldwell, Lee, Macbeth, & Young, 2008). Refer to Figure 1.1 for an overview of the physical influences of testosterone on the body.

1.3.1. Testosterone, social aggression and status

The importance of power to interpersonal relationships and well-being has meant that the effects of testosterone on social behaviour have been a topic of great interest over the last few decades. This surge in research is due, as well, to improvements in assay technologies and the development of hormone administration paradigms (Tuiten, Van honk, Koppeschaar, Bernaards et al., 2000), but perhaps most influentially due to early evidence suggesting that the steroid hormone promotes an aggressive, impulsive form of social dominance (Banks & Dabbs, 1996; Dabbs, Jurkovic & Frady, 1991, 1995; Scerbo & Kolko, 1994; Stålenheim, Eriksson, von Knorring & Wide, 1998; van Goozen, Matthys, Cohen-Kettenis, Thijssen et al., 1998). Indeed, testosterone has acquired a bad reputation in the popular media, with folk ideas still emphasising its role in violence, delinquency and oppression (Barber, 2012; Daoust, 2017; Goleman, 1990; Solon, 2012).

The notion of dysregulation has occupied a prominent place in the literature on testosterone and behaviour. Reactive social aggression, which in less complex animals is a means to power and dominance, is thought to occur as a result of testosterone's ability to dampen functional connectivity between cortical and subcortical structures, including cross-talk between the amygdala and the orbital frontal cortex (OFC) (Schutter & van Honk, 2004; van Wingen, Mattern, Verkes, Buitelaar et al., 2010) – a key substrate of emotional impulse control. Mehta and Beer (2010) have proposed that the testosterone-aggression link can be explained by its ability to reduce activity in this region. Impulsivity tends to be framed as a negative trait, but it may reflect too what Guinote (2017) refers to as having “strong agendas” and being impelled to action.

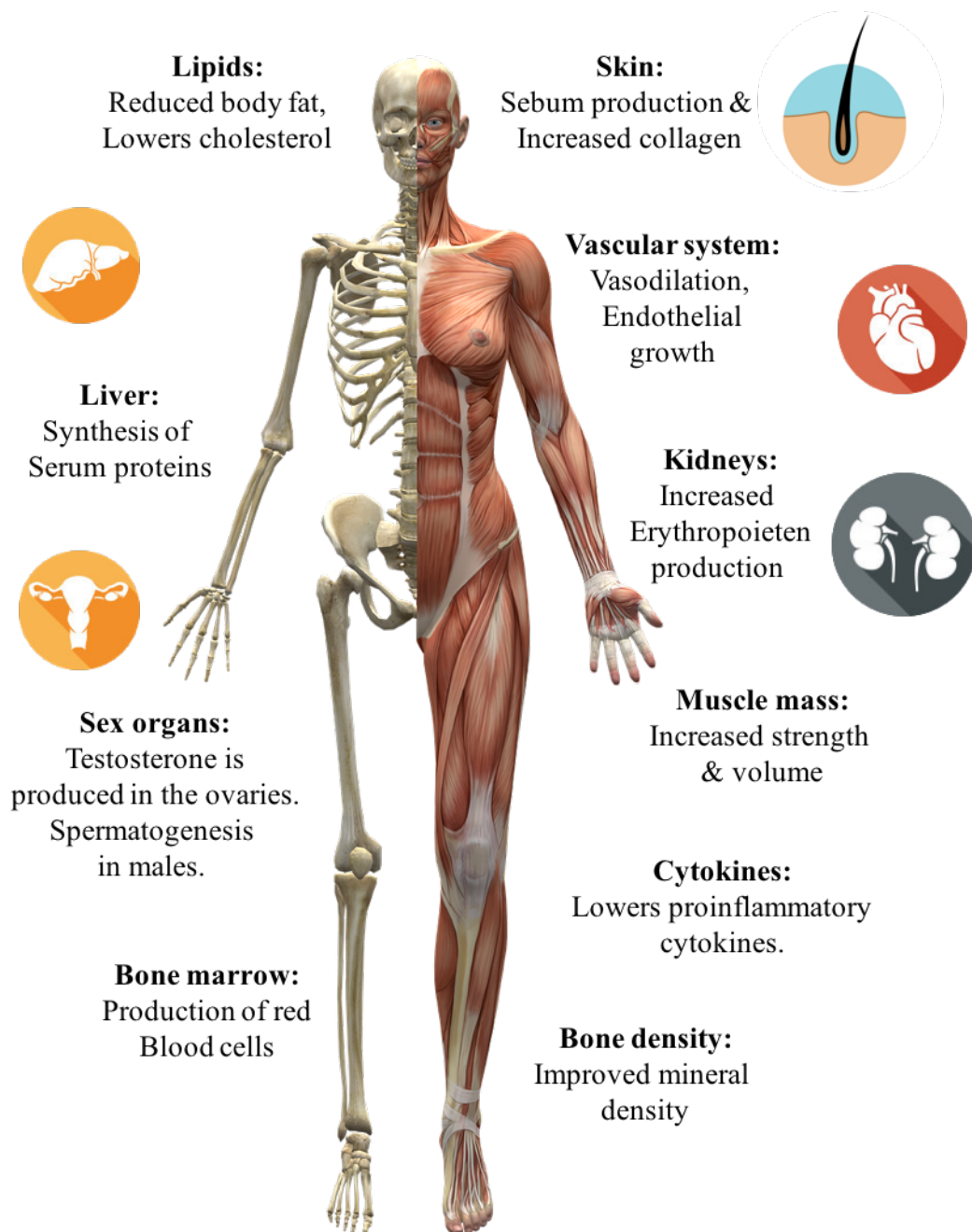


Figure 1.1 The effects of testosterone on the physical body. (Boulanger, 2009; Nieschlag, Behre & Nieschlag, 2012; Malkin, Pugh, Jones & Kapoor et al., 2004; Tambo, Roshan & Pace, 2016; Yesilova, Ozata, Kocar, Turan et al., 2000).

Controlling impulses may involve the internalisation of social codes, these being a vehicle of social management often resisted by powerful individuals (See, Morrison, Rothman & Soll, 2011). Moreover, despite the established link between testosterone and impulsivity (Daitzman, Zuckerman, Sammelwitz & Ganjam, 1978), not all forms of social persuasion

that are fuelled by the hormone are reactive in nature. Van der Westhuizen and Solms (2015b) report a dissociation between trait dominance and rage, the former correlating uniquely with a high testosterone: cortisol ratio. In this study, the experience of overwhelming anger as a personality trait was in fact negatively related to baseline testosterone levels, suggesting that testosterone does not necessarily predispose to “reckless” behaviour. Other work has shown that testosterone actually reduces risky, cold bluffing in a modified Poker game in conditions where display of dominance or status-seeking requires less adventurous or more conservative behaviour (van Honk, Will, Terburg, Raub et al., 2016). This suggests that effects of testosterone strongly depend on the social environment and coheres with recent evidence that testosterone promotes behavioural flexibility (Diekhof & Kraft, 2017), which is a core aspect of emotion regulation.

Considering this, much of the evidence that implicates testosterone in violence and aggression can be interpreted instead to reflect an underlying motivation to gain or maintain high social status (see Eisenegger et al., 2011 for review) – status being a proxy for ability to exert social control. Hence, although aggression can and often does erupt in dominance contexts, this may only occur in situations where control cannot be instated. The institutionalisation of sport in modern day societies is a good example of this dynamic. With strict rules to circumvent reactive aggression and operationalise control, opponents can vie for a socially sanctioned victory. In such contexts, competitiveness has been frequently related to testosterone (Booth, Shelley, Mazur, Tharp et al., 1989; Carré & McCormick, 2008; Salvador, Suay, Martinez–Sanchis, Simon et al., 1999) as has the home advantage effect (Neave & Wolfson, 2003). Indeed, a recent study shows that testosterone positively associates with self-efficacy, which in turn predicts competitive performance (Costa, Serrano & Salvador, 2016).

1.3.2. Testosterone, vigilance to threat and social approach

A considerable body of research provides support for the idea that asserting control via the monitoring of status is a key mechanism via which testosterone regulates emotional demands on the individual. Chief among these strategies is vigilance to social threat. A dedicated vigilance system exists in the brains of all mammals which monitors cues related to social status (Davies, Krebs & West, 2012). The amygdala has been identified as a key brain structure that tracks social threat. Several studies have shown that the administration of

testosterone in men and women successfully up-regulates activity in the amygdala in status-relevant contexts (Goetz, Tang, Thomason, Diamond et al., 2014; Hermans, Ramsey & van Honk, 2008). Interestingly, up-regulated amygdala activation is seen in response to both fearful and happy faces (Bos, van Honk, Ramsey, Stein et al., 2013). This is consistent with contemporary notions that the amygdala is a generalised mechanism for computing social uncertainty (Bossaerts, 2010) – and specifically as a function of immediate contextual goals since the mitigation of uncertainty is seen as a core means toward efficient self-regulation (Sterling & Eyer, 1988). Though, some evidence for a bias toward threatening stimuli is still reported (Cunningham, Van Bavel & Johnsen, 2008).

Most notably, the effect of testosterone on the amygdala response appears to be specifically related to an *approach* emotionality. Testosterone-enhanced vigilance does not serve avoidant or escape strategies, even in women with high trait anxiety (Terburg, Syal, Rosenberger, Heany et al., 2016). In a recent fMRI study, Radke et al. (2015) had participants approach or avoid affective faces by either pulling or pushing a joystick. They found that enhanced amygdala activity following testosterone administration was bound specifically to conditions of approaching social threat, corroborating previous work showing that testosterone elicits cardiac acceleration after viewing angry faces (van Honk, Tuiten, Hermans, Putman et al., 2001). Though pharmacological elevation of testosterone implicitly increases vigilance to masked social cues of threat (Terburg, Aarts & van Honk 2012b), testosterone and AVP also decrease the ability to explicitly recognise negative facial expressions (van Honk & Schutter, 2007; Uzevovsky, Shalev, Israel, Knafo et al., 2012). These combined effects appear to draw attention to signs of threat while simultaneously inhibiting their registration at the conscious level. This may help to suppress fearful or empathic reactions, both of which may present obstacles to self-serving motivations. Testosterone does appear to diminish fearfulness (van Honk, Peper & Schutter, 2005) as well as automatic facial mimicry (Hermans, Putman & van Honk, 2006), “mind reading” (Bos, Hofman, Hermans, Montoya et al., 2016) and the ability to effectively collaborate with others (Wright, Bahrami, Johnson, Di Malta et al., 2012).

In less threatening contexts, androgenic pathways may encourage social approach by biasing attention toward social cues via activation of classical reward-related centres (Macoveanu, Henningsson, Pinborg, Jensen et al., 2016; Weber, Soder, Potts & Bornovalova., 2017). For instance, in young children viewing positively compared to negatively valenced facial

expressions, foetal testosterone, (measured via amniotic fluid), predicts activation in the caudate nucleus, putamen and nucleus accumbens but not in the amygdala (Lombardo, Ashwin, Auyeung, Chakrabarti et al., 2012). Salivary testosterone levels have been shown to increase following exposure to happy faces, though this effect is stronger in response to anger (Zilioli, Caldbick & Watson, 2014). Recent findings demonstrate that such effects of testosterone on perceptual preferences may generalise to other social domains which do not directly involve status. Hahn, De Bruine, Fisher and Jones (2015) have shown that women's endogenous testosterone levels positively predict their ratings of cuteness in babies and Bos, Hermans, Montoya, Ramsey et al. (2010) demonstrate that the hormone up-regulates parental care by acting on the insula, cerebellum and thalamocingulate region. This may serve to promote reproduction and function more generally to encourage pro-social behaviour.

1.3.3. Testosterone and pro-sociality

Indeed, contemporary research paradigms that utilise more nuanced designs to study the motivational properties of testosterone have shown that it does not only promote hostile strategies in the pursuit of power, but is also linked to certain pro-social behaviours that monitor fairness in dominance hierarchies. For instance, a number of studies have found testosterone to be positively related to leadership roles (Dabbs, Bernieri, Strong, Campo et al., 2001; Rowe, Maughan, Worthman, Costello et al., 2004) and while not all leaders are philanthropic, several recent findings support the role of testosterone in facilitating cooperation during social interaction.

Eisenegger, Naef, Snozzi, Heinrichs et al. (2010) reported increased fair bargaining behaviour in the Ultimatum Game in a sample of women administered 0.5mg testosterone. In a similar paradigm, Van Honk, Montoya, Bos, van Vugt et al. (2012) showed increased cooperation after testosterone administration in a Public Goods game in women with high 2D:4D digit ratio. The 2D:4D ratio reflects prior exposure to testosterone and oestradiol in utero, and high 2D:4D ratio points at prenatal oestradiol dominance (Lutchmaya, Baron-Cohen, Raggatt, Knickmeyer et al., 2004; Zheng & Cohn, 2011). Boksem, Mehta, Van den Bergh, van Son et al. (2013) further found that testosterone leads to increased reciprocity during a trust game. Similarly, the administration of the hormone has also been found to decrease the incidence of lying in a die-rolling game (Wibral, Dohmen, Klingmuller, Weber

et al., 2012) but somewhat paradoxically, testosterone also seems to reduce return of trust (Bos, Terburg & van Honk, 2010; Boksem et al., 2013; Carré, Baird-Rowe & Hariri, 2014). Moreover, when provoked with an unfair offer in bargaining games, testosterone does not facilitate social cooperation (Burnham et al., 2007; Mehta & Beer, 2010; Ronay & Galinsky, 2011). The pro-social effects of testosterone thus appear to be strategic and limited to situations involving active negotiation of status.

1.3.4 Summary: Testosterone and social empowerment

Thus, to summarise, the extensive literature on testosterone and social behaviour is multifaceted and sometimes seemingly incongruous but echoes psychological accounts of power as being underpinned by a strongly pro-active, self-investing disposition. Behaviours related to aggression and threat monitoring may operate in the service of maintaining control and independence with a number of detrimental effects to empathy and social cooperation. At the same time, however, recent findings indicate that testosterone plays a critical role in social regulation, both of the self, by way of vigilance to social cues, but also at the group level. Testosterone appears to be important in leadership, in maintaining fairness in social groups and even in reducing risky decision-making. The concept of an incentive for increasing and maintaining social status is therefore consistent with the wider literature on the effects of testosterone on social behaviour. That is, testosterone motivates and empowers individuals in competitive contexts in the service of gaining or maintaining high levels of social control.

1.3.5. A new methodological approach

The motivation for status is a useful one because it describes the continuity in behavioural responding across many different social contexts, yet is less useful in the study of instinctual motivations underpinning the formation of dominance hierarchies and acquisitions of power. This makes it a challenge to appropriately understand what status means in terms of intrinsic biological value to the individual. Indeed, a major obstacle in social neuroscience is the development of definitions that transcend the vagaries of human language and culture. Because “status” and “control” are abstractions, the result is that social intentions can be hard to read in constrained laboratory settings, especially considering that many overt dominance displays and gestures are inhibited by codes of conduct for interpersonal

interaction. What's more is that "competition" need not be formalized or even recognized by researchers to exert influence in social contexts. This is a challenge compounded by the reported difficulty that people have articulating their emotional states following testosterone administration (Eisenegger et al., 2010; Terburg et al., 2012;). Several studies reveal how implicitly operating processes explain many of the effects of testosterone on social behaviour (Terburg et al., 2011; van Honk et al., 2005; van Honk & Schutter, 2007). Studies with explicit methods allowing conscious mediation, e.g. involving self-report or behavioural paradigms contaminated by social desirability biases, have inherent limitations. Testosterone acts implicitly on behaviour, not on what people think about their behaviour. Operational definitions that are able to bypass introspection offer a promising approach to furthering our understanding of the nuances of motivation during social interaction.

The study of testosterone and power is yet to take advantage of the new methodological approaches offered by the field of "embodied cognition," in which the mind in its interaction with the body and environment is seen as a constituting factor in the emergence of *meaning* (Lackoff, 2012; Wilson, 2002). The following section will provide an overview of this theoretical framework and introduce the idea that the defensive, "approach" orientation that is characteristic of dominant behaviour may be facilitated in part by an implicit experience of empowerment and control that is rooted in the basic sensory-motor processes that engender embodiment.

1.4. Embodied cognition

Emerging ideas on the interdependent role of the body and the mind have recently been applied to understand the brain-basis of higher-order concepts, especially those related to perception and feeling states governing social behaviour (Barsalou, 2008; Lackoff, 2012; Varela, Thompson & Rosch, 2017). Embodied or "grounded" theories maintain that mental states are deeply dependent on properties of the physical body interacting with the environment (Wilson, 2002; Witt, 2011). According to these accounts, cognition evolved to support action. Knowledge and value are thus thought to emerge from experiences of the body and take the form of re-enactments of motor, perceptual and other bodily states that are recruited during interaction with objects – social or otherwise – in terms of the range of possibilities that they provide for *use*. For example, an object such as a "mug" is understood

in terms of the actions associated with its use that are simulated in mind in response to seeing its affordances. The meaning of a “mug” is thus captured in these sensory-motor simulations.

Meaning, that is, the value associated with an entity, is not static but depends on the current state of the organism. Cognitive processes such as the perception of distance as ‘far’ or ‘near’ appear therefore to depend in part on the current physical status of the body (Witt & Proffitt, 2008). Fatigue, for instance, has the effect of making objects look further away, less within the capabilities of the acting body. This is thought to occur because the perception of distance is embedded in motor terms and involves the mental simulation of necessary actions in the same motor regions of the brain that coordinate action execution. The status and integrity of bodily representations in relation to specific events in the environment should therefore play a fundamental role in mental experience.

1.4.1. Embodiment of social emotions

Importantly, social abstractions may also have an embodied basis. Eisenberger and colleagues have recently demonstrated that the neural mechanisms of thermoregulation overlap with those involved in feelings of social warmth (Inagaki & Eisenberger, 2013). People may similarly use embodied associations to understand what it means to be socially excluded. As humans, our sensitivity to cold may have less to do with physiological regulation and more with social regulation. Ijzerman, Gallucci, Pouw, Weißgerber et al. (2012) observed that rejection in a group game lead to decrements in limb temperature. Likewise, the experience of mental pain appears to gain some of its phenomenal quality from the fact that it shares brain substrates with those that regulate physical pain (Eisenberger & Lieberman, 2004).

The idea that our experience of the environment and appreciation of abstract concepts is modelled on our sensory and motor processes is not a new one, but is somewhat controversial as it goes against traditional theories which maintain that cognition occurs independently from behaviour, providing a fixed, objective representation of the world (Wilson, 2002). However, research is accumulating to suggest that studying perceptual and motor representations can enrich our understanding of many facets of perceptual and emotional experience. For instance, the literature on empathy has benefited enormously, both empirically and conceptually, by the discovery of mirror neuron circuits which activate when

observing another social agent, simulating their movements and gestures (Fadiga, Craighero & Olivier, 2005; Gallese, Fadiga, Fogassi & Rizzolatti, 1996; Rizzolatti, Fadiga, Fogassi & Gallese, 1999). In this way, the recognition and understanding of what it feels like to be that person emerges out of one's own motor experience. Research on the role of testosterone in social emotion can similarly gain from the inclusion of the embodied paradigm in answering the question of how social status comes to be represented in the brain. Since status enables control over the social environment, neural systems that sub serve action through motor control may be a good place to start in thinking about the embodied basis of status-related cognition and emotion.

1.4.2. The representation of status in the brain

Neural maps of the body that function to control behaviour during social interaction may provide insight into how power and status are represented in the brain. For a start, it is perhaps not coincidental that our colloquial linguistic references about these concepts relate in many ways to the terminology used to describe the navigation of the body in the 3-D environment. We speak of 'high' status, the 'upper' echelons of society and winning positions as being 'one up' or being 'ahead' and not 'behind'. Gagnon and colleagues (2011) have provided empirical support for this association. They showed that performance on an implicit association test was facilitated when participants were required to pair high status concepts with mountainous topography and with North-pointing compasses compared to level terrain and cardinal south.

The association between social status and height ("up") may have its roots in development from the experience of being largely immobile and helpless as a baby on one's back with larger, more powerful figures looking over from the top. Infancy, of course, is a time before motor control has been established. Importantly though, the first signs of "proto-dominance", expressed in the form of possessive behaviour, emerges from the unfolding of basic sensory-motor proficiencies. As infants develop postural control and effective reaching behaviour, they begin to use objects in the environment as a means to gain control over their social situation by capturing the gaze of another (Rochat, 2010). If caregivers fail to respond appropriately, the infant may struggle to attain a sense of mastery over their social environment (Murray, 1985; Nadel, Carchon, Kervella, Marcelli et al., 1999; Rochat, 2001).

Being largely incapacitated, these first experiences of agency depend on the coordinated cooperation of other social agents. Prior to these achievements however, the instinctual proclivity to ‘latch on’ in response to contact paves the way for the development of a basic sense of ownership over the body, which is required for the emergence of motor control and even basic manifestations of possessiveness (Rochat, 2010). Testosterone may contribute to embodied capacity and the ability to possess from early on. For example, Field, Whishaw and Pellis (2000) have documented sex differences in the motor organization of postural support, which appears to relate to early effects of gonadal hormones on the brain. Critically, Rochat, Goubet and Senders (1999) note, the inclination to reach out and claim ownership of objects in the environment only emerges once postural stability has been established.

Later in life, these same motor competencies may in turn affect cognitive functioning in ways that are advantageous for competition. For instance, the appraisal of a physical challenge, such as a climbing wall, is known to activate a pattern of motor simulations that correspond to the required manoeuvres (Pezzulo, Barca, Bocconi & Borghi, 2010). Successful recall of the route in memory has been shown to depend on motor competency, and not perceptual salience of the route, suggesting that the integrity of the motor system has meaningful effects on the cognitive tasks that support competition. For instance, the experience of physical equilibrium, of bodily stability, may be recruited to communicate the concept of balance in the higher-order domains of fairness and entitlement, and even psychological equilibrium (Johnson, 1987). Assertiveness may similarly emerge out of sensory-motor representations of the body. For example, independent of its physiological effects, the advantages of testosterone to competitive performance have been suggested to emerge from improved signalling of effort or the “readiness to perform” (Cook & Beaven, 2013). Animal studies provide some support for a role for “readiness” signalling. Experiments in rats have shown that restraining the physical body during exposure to electric shock leads to increased physiological signs of threat and withdrawal (drop in blood pressure, elevated heart rate) while unrestrained rats demonstrate signs of behavioural resilience (maintenance of blood pressure, elevated heart rate) (Iwata & LeDoux, 1988). Thus, even though the fear-evoking stressor was the same, the state of the body was the determining factor in freezing versus escaping.

These observations and those from the developmental literature emphasise the fundamental role of sensory-motor representations that develop to acquire control and ownership over the

body as a platform from which to experience and appraise control in the social world. Some evidence implicates testosterone in this relationship (Cook & Beaven, 2013; Field, Whishaw & Pellis, 2000), however, no studies to date have formally explored this link and studies are only now beginning to examine the role of embodiment in social power (e.g. Moeini-Jazani et al., 2017).

The following sections will introduce three ways that the brain maps the body and its actions, which may be of particular interest to our understanding of how status and power are represented and regulated in the brain. These processes include 1) Interoceptive awareness, 2) Body ownership, and 3) Sensorimotor agency. Given that perception invokes the recruitment of bodily representations in order to assess the opportunities and limits brought to bear by the immediate external environment, from the outset, the neural network that dynamically represents the entire body in relation to the changing environment, that is, the peripersonal space (PPS; Fogassi, Raos, Franchi, Gallese, Luppino & Matelli, 1999; Makin, Holmes & Zohari, 2007; Mishkin, Ungerleider & Macko, 1983), was additionally identified as a potentially important embodied mechanism for regulating approach/avoidance motivation and representing ownership and social instability (Brozzoli Pavani, Urquizer, Cardinali et al., 2009; Graziano & Cooke, 2006; Heed, Habets, Sebanz & Knoblich, 2010; Sambo, Liang, Crucci & Iannetti, 2012; Teneggi, Canzoneri, Pellegrino & Serino, 2013). The investigation into the effects of testosterone on PPS mapping is ongoing in our group, but due to logistical reasons, could not be included for submission in the current body of work. Likewise, other processes such as proprioception, for example – the sense of the body's positioning in space – deserves mention in discussions of the embodiment of power. Harmon-Jones and Peterson (2009) report interesting findings showing that being in an upright versus supine position increases the neural response to anger. Technological, financial and time constraints limited the scope of this work to just three dimensions of embodiment, which were favored not only due to the extent of the general literature that has already accumulated on each respective topic, including the ways in which they interrelate, but because they represent three fundamental dimensions of embodiment: the internal body (interoceptive awareness), the external body (body ownership) and the body acting in space (sense of agency). Once a basic picture of the effects of testosterone on these important aspects of embodiment have emerged, future investigations can be designed in more nuanced ways to add depth to our understanding of the topic.

1.5. Interoceptive awareness

Social threat might be processed in the brain in very similar ways to deviations in the body's homeostatic balance. That is, social gains and losses may come to be known and experienced in ways comparable to biological loss and therefore studied using similar approaches. If this is the case, one would expect some degree of modulation by testosterone to the systems regulating allostasis.

1.5.1. Definition and measurement

The interoceptive system helps to monitor homeostasis. Interoception refers to the awareness of signals arising from various organs and systems within the body and provides a sense of the physiological condition of the body (Craig, 2002). Neuroanatomical investigations have identified several pathways that give rise to interoceptive representations. This network comprises peripheral receptors and nerve fibres carrying sensory information (C-fibre afferents) which terminate monosynaptically in lamina I of the spinal and trigeminal dorsal horns of the spinal column. In this way, information about the thermal, mechanical, chemical and hormonal status of the viscera, muscles, joints, teeth and skin are conveyed and projected to pre-autonomic thalamic sites in the brain stem and are eventually integrated in a posterior-to-mid-to-anterior pattern in the insula cortex (Craig; 2002; Craig, 2009), as well as the anterior cingulate cortex (ACC) and limbic motor cortex (Vaitl, 1996; Bush, Luu & Posner, 2000; Vuilleumier, 2005; Critchley, Wiens, Rotshtein, Öhman, 2004).

Some conceptions of interoception go beyond visceral afferents and include sensations from other internal body receptors, such as circulating chemicals, proprioceptive inputs and C-tactile somatic receptors of the dermis which monitor feelings of pleasure or warmth from affective touch (Björnsdotter, Löken, Olausson, Vallbo et al., 2009). Photoreceptor cells of the eyes are also considered by some to form part of the interoceptive system (Lucas, 2013).

Concentrations of GABA (γ -aminobutyric acid) in the insula cortex have been associated with subjective interoceptive awareness (Wiebking, Duncan, Tiret, Hayes et al., 2014). Another study found that cortisol increased processing in the brain of heartbeat evoked potentials (Schultz, Strelzyk, de Sá, Naumann et al., 2013). Importantly, subjective awareness of bodily signals may reflect only one dimension of interoceptive processing.

People may differ in terms of the extent to which they pay attention and respond to bodily sensations, the magnitude of these sensations and the degree to which metacognitive perceptions of detection accuracy correspond with accuracy on objective testing (Garfinkel, Seth, Barrett, Suzuki et al., 2015). While there is some data on the chemical foundations of subjective awareness of interoceptive signals, very little is known about the neurochemical control of interoceptive accuracy.

Tests have been developed to measure interoceptive accuracy, such as the Schandry method, a heartbeat detection paradigm in which subjective counts of heart beats within allotted intervals are compared to objective tallies (Schandry, 1981). Heart beat monitoring of this kind has been found to correspond with other measures of interoceptive accuracy such as tests of gastric acuity (Herbert, Muth, Pollatos & Herbert, 2012), however, it is unknown for the most part how the various interoceptive constructs across bodily domains (heartbeat versus respiration, blood glucose, temperature etc.) relate to each other. In keeping with an embodied cognition account, certain stimuli may induce unique bodily responses to convey specific kinds of information and emotional traits may exert selective impact in each domain. For instance, depressed individuals might experience changes in thermoregulation more acutely and perceive these signals more accurately than gastric sensations (Hanusch, Janssen, Billheimer, Jenkins et al., 2013; Izjerman et al., 2012). This poses great methodological challenge.

1.5.2. Interoception and emotion regulation

Interoception is an iterative process which informs response selection and motivated behaviour (Craig, 2008). Higher-level goals and prior learning are in continuous interaction with afferent sensory signals to valence emotional reception of these signals and direct self-regulatory behaviour (Craig, 2009). In this way, sensations of the bodily self, that is, minimal phenomenal consciousness, becomes laden with motivational imperatives. This is argued to be the basis of selfhood – the neural monitoring of internal organs and sensations in relation to current needs (Damasio, 1999; Park & Tallon-Baudry, 2014). Interoception is therefore intimately linked to the control of action (Gu & Fitzgerald, 2014) via interaction with affective processes (Barrett, Quigley, Bliss-Moreau & Aronson, 2004; Wiens, 2005). At the same time, behaviour, emotions and cognitive styles impinge on the availability of bodily sensation. For example, accuracy in detecting internal signals increases after short-term food

deprivation (Herbert, Herbert, Pollatos, Weimer et al., 2012) and by focusing attention on physical or autobiographic aspects of the self (Ainley, Maister, Brokfeld, Farmer et al., 2013) but appears to decline under stress (Fairclough & Goodwin, 2007) and following the experience of social rejection (Durlak & Tsakiris, 2015). Such modulation may therefore gate the extent to which interoceptive information is able to inform approach or avoidance decision-making, especially in the face of threat.

Interoceptive processing may regulate “approach” because the ability to successfully anticipate threat to homeostasis may depend on the accuracy with which interoceptive signals are perceived (Pezzulo, Rigoli & Friston, 2015). This follows from the idea that in order to efficiently address perturbations in the body’s equilibrium through goal-directed behaviour, i.e., to exert appropriate control, information about the existing condition of the body must come into awareness. For example, deficits in the ability to generate or represent signals of arousal have been linked to maladaptive decision-making (Bechara, 2004; North & O’Carroll, 2001) while accuracy in interoceptive awareness is associated with advantageous decision-making (Werner, Jung, Duschek & Schandry, 2009), better self-regulation (Füstös, Gramann, Herbert & Pollatos, 2012; Herbert, Ulbrich & Shandry, 2007b) and flexibility and focus of attention (Matthias, Schandry, Duschek & Pollatos et al., 2009).

1.5.3. Interoception and threat monitoring.

This body of evidence, together with the fact that the processing of bodily signals does form a core component of many theories of emotion and regulation (Damasio, 2010; James, 1884), suggests that vigilance to cues of social threat may also be affected by interoceptive processing. Garfinkel, Minati, Gray, Seth et al. (2014) have shown that both amygdala activation and the recognition and intensity of threatening cues is enhanced by simultaneous processing of interoceptive signals. Further evidence to support this idea comes from imaging studies showing that both interoception and social threat processing are linked to activity in the insular cortex. For instance, during bargaining in the Ultimatum Game, Sanfey, Rilling, Aronson, Nystrom et al. (2003) have shown that when an unfair offer is received, the insula cortex activates. A number of studies also report activation of the insula by testosterone under various emotional conditions (Bos et al., 2010; Chen, Chen, Decety, Huang, et al., 2016; Lentini, Kasahara, Arver & Savic 2013), suggesting that it may in turn affect interoceptive awareness to guide responses to threat. Of note, is that testosterone is

known to increase the rate of rejection for unfair bargaining offers (Mehta & Beer, 2010), as is the case in individuals who score higher on interoceptive measures (Dunn, Evans, Makarova, White et al., 2012). Corroborating this, a recent study found that highly accurate interoceptors tend also to be particularly averse to the experience a loss (Sokol-Hessner, Hartley, Hamilton & Phelps, 2015).

These findings raise the possibility that the influence of testosterone on vigilance to cues signalling social challenge may occur in part via its modulation of interoceptive awareness, which guides decision-making and approach motivation in response to threat. In support of this idea, interoceptive processing has shown to be sensitive to social status. For example, social ostracism by exclusion in the Cyberball Game (Williams, Govan, Croker, Tynan et al., 2002) leads to a drop in interoceptive accuracy (Durlak & Tsakiris, 2015). The meaning of social loss seems to be captured by a loss in awareness of the bodily self. Rejection in this game also causes a decline in baseline testosterone levels in both men and women (Radke, Seidel, Boubela, Thaler et al., 2017; Seidel, Silani, Metzler, Thaler et al., 2013). Thus, the experience of social disempowerment appears to reflect in changes in hormones in ways that mimic changes in interoceptive awareness.

1.5.4. Interoception and performance.

This link between interoceptive processing and some of the functions of testosterone calls for consideration of whether or not accurate perception of bodily signals has any bearing on success in competitive contexts? Paulus and colleagues (2009) have proposed that faulty interoceptive information undermines performance in challenging environments because of a mismatch between the experienced state of the body and the necessary action that is required to restore homeostasis. More importantly, uncontrollable threat in the form of error signals conveyed by the insula in response to mismatches is thought to be intrinsically anxiety-provoking (Paulus & Stein 2006). Interestingly, this destabilization reflects at the level of the body schema, with low interoceptive ability linked to more malleable external body representations (Tsakiris, Tajadura-Jimenez & Constantini, 2011). Though earlier work suggested a positive link between interoceptive accuracy and anxiety (Domschke, Stevens, Pfleiderer & Gerlach, 2010; Pollatos, Herbert, Kaufmann, Auer et al., 2007; Wells & Papageorgiou, 2001), this relationship is apparently not so straightforward. Accumulating

research shows that individuals with better interoceptive accuracy tend to have an advantage in regulating their emotions in distressing situations (Fustos et al., 2012; Kever, Pollatos, Vermeuleun & Grynberg, 2015; Pollatos, Matthias & Keller, 2015; Werner, Kerschreiter, Kindermann & Duschek, 2013). Reduced interoceptive ability has been related to obsessive-compulsive disorder (Weiss & Pollatos, 2014), clinical depression (Dunn, Dalgleish, Ogilvie & Lawrence, 2007), poorer self-regulation in somatoform patients (Weiss et al., 2014) and indecisiveness (Furman, Waugh, Bhattacharjee, Thompson et al., 2013). In general, these studies point to the important role of interoceptive accuracy in assertive coping efforts. The ability of testosterone to increase tolerance for risk and promote approach behaviour in response to threat suggests that fluctuations in testosterone may in turn influence the representation of interoceptive signals, or vice versa.

The implicit or unconscious nature of many of the reported effects of testosterone as well as its close link to insula activity and threat monitoring, positions it well as a potential modulator of interoceptive functioning, known to be an important mechanism in self-regulation. This hypothesis is supported by the reported sex difference in interoception. More frequently, males are reported to show higher levels of accuracy (Cox et al., 1985; Harver, Katkin, & Bloch, 1993; Katkin, Blascovich, & Goldband, 1981; Koch & Pollatos, 2014), though not all studies find an effect of gender (Rouse & Jones, 1988; Schneider, Lyons & Williams, 2005). Future studies that directly assess the effect of testosterone on interoceptive accuracy will offer useful insight into how power manifests in and interacts with brain/body processes.

1.6. Body ownership

The body is not only processed from within. Exteroceptive signals from the outside are key to understanding the feeling that this body is *mine* (Gallagher, 2000; Tsakiris, Schütz-Bosbach & Gallagher, 2007) – “mine” being conceivably the most rudimentary expression of a territorial imperative. If power emerges from or in conjunction with processes that influence ownership of the body, one might expect some degree of modulation by testosterone.

As a term, body ownership refers to the pre-reflective experience of being the subject of a physical body, the object in space where collisions tend to cause a corresponding,

subjectively experienced sensation (Tsakiris, 2016). When this happens, brain imaging studies have shown related activity in regions such as the insula cortex (Farrer & Frith, 2002; Tsakiris, Hesse, Boy, Haggard et al., 2006), the premotor regions, the cerebellum (Ehrsson, Holmes & Passingham, 2005), and also the parietal cortices (Ehrsson, Spence & Passingham, 2004).

That the feeling of body ownership has to do with this kind of “sensory correlation” is a phenomenon substantiated in experimental work showing that the synchronous registration and integration of bodily signals within these brain regions gives rise to subjective feelings of body ownership (Lopez, Halje & Blanke, 2008; Ehrsson, 2012; Tsakiris, 2008; 2010). These signals are diverse and hierarchical, involving the integration of exteroceptive visual information about the physical body with top-down models of a “body matrix” (Moseley, Gallace & Spence, 2012; Riva, 2017) as well as bottom-up signals from somatosensory, auditory, vestibular, visceral, motor and affective sources (Damasio 2000; de Vignemont, 2011; Ehrsson, Spence & Passingham, 2005; Metzinger 2003). Refer to Figure 1.2 for an overview of how this integration process might work.

Despite this complexity, that our body is *ours* is normally taken for granted, though this is not the case in pathological conditions causing damage to certain parts of the brain (Valar & Ronchi, 2009) or in individuals younger than 18 months of age who have not yet achieved explicit self-awareness (Bertenthal & Fischer, 1978). Only mid-way during the second year of life do young children begin to recognize themselves in the mirror, imbued with the feeling that this acting body is “me” and those things beyond its confines, “not me”. However, there is evidence that pre-conscious recognition of the bodily self is there from birth (Rochat, 1998; Rochat & Striano, 2000).

1.6.1. Body ownership and the innate potential to adapt.

According to Merleau-Ponty (1967), the infant perceives from very early on the forms and patterns of the “whole body posture” in relation to the forces exerted on it by both the external and internal environment – not only gravitational pull and sensations from the outside, but also affective and homeostatic pressures from within. There are findings to support this proposal, such as in studies of the head orienting response of hour-old babies,

which are initiated more reliably in response to external tactile stimulation of the cheek than when the infant's own hand spontaneously brushes its face (Rochat & Hespos, 1997). Gallese and Sinigaglia (2010) have further argued that achievement of bodily self-recognition occurs not merely through a process of sensory-motor perceptual association, but through the pre-reflective experience of the body's innate *potential to act*, even when action is not necessary or not even possible (Fotopoulou, Tsakiris, Haggard & Vagopoulou et al., 2008). Thus, ownership of the body tends to be construed in terms of explicit self-identification but ownership also operates at the implicit level from early on.

From a neuropsychological perspective, the early achievement of an innate sense of body ownership speaks to its profound adaptive functions. Body ownership not only establishes self-location from an egocentric visuo-spatial perspective, but it is also a mechanism that allows the subject to organize information in rapidly changing settings (Graziano & Botvinick, 2002; Metzinger, 2003; Neisser, 1988). This in turn enables efficient interaction and a sense of familiarity or constancy. For instance, Banakou and colleagues (2013) have shown that body ownership affects visual processing. Adult participants experimentally induced to experience ownership over a child's body begin to over-estimate the physical size of objects and experience themselves in more child-like ways (Banakou, Grote & Slater, 2013). The physical body mediates all experience with the outside environment throughout one's lifetime and in this way forms the bedrock of a coherent autobiographical, narrative self (Gallagher, 2000).

Research in the clinic provides evidence of the profound disturbances to the self when body ownership is disrupted. In neurological cases like *somatoparaphrenia*, where patients lose the feeling of ownership of an otherwise healthy, functioning limb, their reaction to the affected limb tends to take the form of extreme hostility or psychosis (Haggard & Wolpert, 2005). In moments of minimal insight, the limb is perceived to be unnaturally "heavy", "voluminous" or "swollen" (Vallar & Ronchi, 2009). In such cases, patients often cease initiating action with the limb despite preserved motor potential. Studies have further demonstrated a reduction in the physiological response to an approaching threat toward the affected limb (Romano, Gandola, Bottini & Maravita, 2014). Ownership of the body therefore appears to play a critical role in the experience of physical integrity and self-regulation, especially so in that it provides a reference point from which to appraise and

actively respond to different kinds of stimuli in the immediate environment, including those that might be dangerous.

The predictive coding framework provides a Bayesian model of brain function (Clark, 2015; Friston, 2010) and is increasingly drawn upon to explain how sensory information interacts with higher-order beliefs to engender embodiment experiences (Apps & Tsakiris, 2013; Seth et al., 2011; Seth, Suzuki & Critchley, 2012; Suzuki et al., 2013). The model proposes that any given change within the nervous system is formulated in terms of matches between incoming sensory data and the brain's "best guess" about the hidden environmental causes of this change. If a guess - a probabilistic prior prediction - poorly explains the sensory data, prediction errors occur and these get passed up to higher levels in the cortex where they can be resolved. In hierarchies of this sort, only the "newsworthy" bottom-up data propagates up the hierarchy. In other words, only data that was not previously predicted passes up in the hierarchy as prediction error. When there is no more error or mismatch, a percept is formed. Importantly though, in the matching process, the influence of prior beliefs and prediction errors on a final percept is weighted probabilistically. This is referred to as *precision*, which encodes the uncertainty or 'inverse variance' of the probability distribution associated with the incoming sensory data (prediction error) and predictions about its causes (Friston, 2009). Thus the brain computes two types of estimates: predictions about the causes of sensory data and a second-order estimate of the precision - or reliability - of both priors and bottom-up data. Sensory data that is easily guessed has high precision. Precise prediction errors here, resulting from mismatches (driven by an imprecise *prior*), have the effect of updating the imprecise prior. A percept is formed when prediction error is resolved at all levels of the hierarchy. This is called *perceptual inference*. If sensory information has low specificity and is estimated to be unreliable (low precision), any prediction errors that result during the matching process are likely to be suppressed. Priors in this case will not change. Precise prediction errors may not only have the effect of updating faulty priors, but they may also be resolved via *active inference*. This may occur especially in cases where priors themselves are estimated to be precise. Active inference describes the process of taking action to "re-sample" sensory evidence in the environment so as to confirm or adjust prior predictions (Brown et al., 2011). Predictive coding has been applied broadly to explain the integration of cues that explain, for example, the sense of agency (Friston et al., 2013) and body ownership (Apps & Tsakiris, 2013). Recently, this framework has also been applied to interoception (Seth, 2013). In this model, accuracy in perceiving visceral signals can be explained in terms of precise interoceptive predictions. Alternatively, it is possible too that strong, and therefore precise, physiological signals lead to increased prediction error that pass up the hierarchy to alter predictions and thereby render the interoceptive percept. Thus, precision within the broader system presents itself as an important mediator of perception and experience. According to Feldman and Friston (2010), precision can be learned, but it appears too that it may depend on neuromodulators (Moran et al., 2013). This suggests a possible role for testosterone, especially given that oxytocin has already been proposed to play a modulatory role (Quartrocki & Friston, 2014). Predictive coding may help to explain, for example, the mechanisms that drive vigilance to threat when testosterone is high. Attention appears to interact with precision - we attend preferentially to precise, reliable signals but at the same time, surprise harnesses attention and attention has the effect of elevating the precision of predictive errors associated with that data (Jiang, Summerfield, & Egner, 2013).

Figure 1.2. Theoretical Box: Overview of Bayesian Predictive Coding

1.6.2. Body ownership and defence

The implicit relationship between body ownership and defence is perhaps best exemplified in a statement by Damasio (2003) where he proposes a definition of the “self” as “whatever the immune systems defines as being part of the body” (p.227). Ownership defines the region of space where foreign objects are able to recruit the brain’s defensive response. This has been most notably demonstrated in studies of body illusions, where experimental procedures induce the feeling of ownership over “not me” body parts and even whole bodies (Salomon, Lim, Pfeiffer, Gassert et al., 2013; Tsakiris, 2017). These studies show that representations of body ownership are not rigid, but can extend to accommodate other bodies and in this way, provide a means through which to study the responsiveness of the systems involved in defending the integrity of the bodily self.

In an experimental procedure referred to as the rubber hand illusion (RHI; Botvinick & Cohen 1998), synchronous stroking of one’s own unseen hand and a rubber hand that is anatomically aligned with the body, leads to a feeling of ownership over the prosthesis as well as changes in the existing bodily matrix. This is thought to occur because of visual dominance in multi-sensory integration (Tsakiris & Haggard 2005), an effect that appears to be robust to distinctions in size (Preston & Ehrsson, 2014), age (Banakou, Groten & Slater, 2013), gender (Slater, Spanlang, Sanchez-Vives & Blanke, 2010) and race (Maister, Sebanz, Knoblich & Tsakiris, 2013). The extent of the illusion can be quantified in three ways: by the subjective, self-reported feeling of ownership (Botvinick & Cohen 1998; Longo, Schüür, Kammers, Tsakiris et al., 2008), by a shift in subjective perception of the real limb’s location towards the rubber hand (proprioceptive drift; Botvinick & Cohen 1998) and by changes in physiology such as an objective drop in temperature in the real hand (Hohwy & Paton, 2010; Kammers, Rose & Haggard, 2011; Moseley et al., 2008; Thakkar, Nichols, McIntosh & Park, 2011; Tsakiris, Tajadura-Jiménez & Constantini, 2011; Van Stralen et al., 2014).

Injuring a perceptually embodied rubber prosthesis has been shown to elicit a skin conductance response in the real hand (Armell & Ramachandran, 2003). Similar findings have emerged in other research – Ehrsson and colleagues (2007) found that threatening a rubber hand lead to increased activity in brain regions associated with anxiety and defensive monitoring, such as the insula and anterior cingulate. This response was found to be positively related to the extent to which participants experienced ownership over the

prosthesis. Importantly activity in motor regions was also found to corresponded with the urge to retract the rubber limb. These findings establish body ownership as an important mechanism regulating the brain's response to threat and therefore imply a potential role for testosterone.

It is possible, however, that threat reactions do not occur as a result of ownership *per se*, but instead reflect affective resonance, a mirror mechanism in which a simulation in one's own brain is run to understand the actions and experiences of a perceived other (Rizzolatti et al., 1999). For example, witnessing another person receive a painful stimulus has been found to activate identical brain areas that activate for self-pain (Morrison, Peelan & Downing, 2006). Nonetheless, these studies highlight the capacity of bodies to elicit alarm. For humans, the importance of social affiliation means that defending the bodies of others has been strongly selected for during evolution. This tendency, generally referred to as the CARE system (Panksepp & Biven, 2012), is a critical social emotion that facilitates social bonding and other altruistic behaviours. Not surprisingly, there is evidence to suggest that malleability in some domains of body ownership appears to be a function of empathic motivation (Asai, Mao, Sugimori & Tanno, 2011; Cascio, Foss-Feig, Burnette & Heacock 2012; Paton, Hohwy & Enticott, 2012). For instance, Ide and Wada (2017) recently found that salivary oxytocin, which is well known for its role in social nurturance and empathy (Insel & Young, 2001; Watt, 2005), positively relates to the degree of subjective ownership in the RHI. This kind of self-other blurring has been shown to reduce implicit racial bias (But see for example, De Dreu, van Kleef, Shalvi & Handgraaf, 2011). Maister, Sebanz, Knoblich and Tsakiris (2013) found that in the RHI, white participants' subjective sense of body ownership over a dark-skinned rubber hand lead to more positive inter-racial attitudes.

1.6.3. Malleable bodies, malleable minds?

A malleable body schema may facilitate caring behaviour via the merging of the body's own "cues" for protection with representations of the other, but it may also predispose to certain passivity phenomena. For instance, a study by Paladino et al. (2010) on multisensory integration in the enfacement illusion, a facial analogue of the RHI, showed that following the induction of an illusory feeling of ownership over another person's face, participants not only rated the other as more attractive and physically similar but were also more influenced by the embodied "other". They tended to defer to their judgement. Individuals with malleable

body representations, where other bodies are able to *replace* own body parts (Guterstam & Ehrsson, 2012), may act in altruistic ways to the detriment of self-serving needs. This is in accordance with embodied cognition theory, where perception and implicit attitudes toward stimuli in the environment manifest by way of, or in relation to the body (Niedenthal, Barsalou, Winkielman, Krauth-Gruber et al., 2005). Studies in phenomenology, a term that refers to the structure of consciousness in terms of the first-person perspective (i.e. what *it is like* to be in a specified state) further argue that bodily signals of all kind constrain one's experience in the world, even when the signals are outside of awareness (Gallagher & Aguda, 2015). It follows that a loss at various levels of the bodily self will have profound implications for self-serving behaviour – a loss, for example, in “gut” feelings which are important for guiding adaptive behaviour (Dunn et al., 2010). Tsakiris and colleagues (2011) have shown that people with malleable body schemas tend to score lower on measures of interceptive awareness, suggesting reduced access to important bodily messages. In contrast, individuals more focused on, aware of and incentivised by their own thoughts and bodily feelings tend to be more powerful (Moeini-Jazani et al., 2017; Van Kleef et al., 2015).

1.6.4. Body disownership and dysregulation

There is some debate as to whether the RHI and other bodily illusions are able to induce disownership of the body (i.e. replacement by the foreign limb) or instead reflect a case of “supernumerary limbs”. Schutz-Bosbach, Tausche, and Weiss (2009) have challenged the disownership account on the basis of their findings in which they have shown that introducing a sensory conflict in the form of observed-*rough* versus smooth-*felt* tactile stimulation not only has no interference effect on the illusion but the experience of the RHI also fails to cause any top-down modulations to the qualitative feeling of the stimulation on participant's own hand. If the real hand is lost, it should not continue to register the quality of tactile stimulation. De Vignemont (2011) points out that too few studies take seriously a possible dissociation between subjective experiences and other measures like proprioceptive drift, and that the idea of disownership may rest purely on data derived from self-report or phenomenological paradigms (Lewis & Lloyd, 2010; Moguillansky, O'Regan, & Petitmengen, 2013).

However, a growing number of studies demonstrate various manifestations of physiological dysregulation in the real limb when the illusion of ownership over the rubber hand occurs. For instance, Barnsley et al. (2011) have shown that histamine activity elevates in the biological hand following induction of the illusion and that the strength of this relationship depends on vividness of the subjective experience. Because histamine reactivity reflects the innate response of the immune system, which operates in the service of detecting non-self entities, these findings suggest that the biological limb starts to be rejected, as if it was a foreign part. This idea of rejection is supported by findings from Moseley et al. (2008) who found that limb temperature in the real hand drops in response to the illusion, an effect possibly explained by a reduction in blood flow to the hand. Though not all studies observe such an effect (de Haan et al., 2017), several have (David, Fiori & Aglioti, 2014; Grynberg & Pollatos, 2015; Hohwy & Paton, 2010; Kammers, Rose, & Haggard, 2011; Moseley, Gallace, & Spence, 2012; Rhode et al., 2013; Tsakiris, Tajadura-Jiménez & Constantini, 2011) to the extent that changes in temperature are often regarded as useful way to operationalise the RHI. To understand how such disownership effects can be achieved, Moseley et al. (2012) have put forward the concept of a “body matrix”, that is, a dynamic neural representation of the body and the space around it that plays a central role in directing homeostatic control of the body.

Debates about disownership aside, changes in the conception of the bodily self appear able to influence homeostatic regulation and should therefore have important implications for adaptive behaviour. Kilteni and Ehrsson (2017) have shown that the sense of body ownership appears to drive the attenuation of self-touch signals – sensory attenuation being a signal of self-generated action because the brain predicts the consequences of one’s actions, leading to a reduction in the expected sensation. These results appear to suggest that body ownership plays an important role in updating the internal representation of the body, which during voluntary action provides the input to the forward model that generates sensory predictions and prepares one for action. Under the influence of a bodily illusion, the real limb appears to be excluded from this sort of preparation. Della Gatta, Garbarini, Puglisi, Leonetti et al. (2016) demonstrated a significant reduction in the amplitude of motor-evoked potentials in the real hand in response to a transfer of subjective ownership in the RHI. In their experiment, when a participant perceived the fake limb to be their own, the region of the brain that controls hand movement was less able to activate the muscles of the real hand.

In sum, changes in body ownership and a blurring of self-other boundaries can have several compromising effects on behaviour, especially in settings where rapid motor responses or sensory-motor simulations would provide significant advantages to overall decision-making and performance. Some of the inconsistencies in the reporting of physiological dysregulation in the context of bodily illusions further suggest that such effects may be mediated by third-variable factors. The close ties between body ownership and defence provide preliminary evidence that emotional factors may be involved. Given the strong links between testosterone, power and defence, a potential role of the hormone in the modulation of body ownership warrants exploration.

1.7. The sense of agency

The feeling of ownership over the physical body has been shown to have important implications for action and self-regulation. But an equally essential dimension of embodiment involves the sense of ownership over the effects that voluntary actions produce. This experience is referred to as the *sense of agency* (SoA) and is defined as the feeling that arises when effected changes are attributed to one's own actions and not to other factors or persons (Haggard & Tsakiris, 2009). It is this implicit understanding of having the ability to effect change that sustains flexible, goal-directed behaviour, the kind that requires more than a single motor response to achieve a desired outcome. Declerck, Boone and De Brabander (2006) argue that the establishment of "if-then" contingencies between actions and their resulting outcomes enables one to develop a sense of control over the environment. Though implicit experiences of agency are seldom explicitly reflected upon, many regard it as the basis of the feeling of "free will" (Wegner, 2004; Wegner & Wheatley, 1999) and its disturbance has been linked to a variety of psychopathologies related to feelings of control, such as depression, schizophrenia and obsessive-compulsive disorder (Gentsch, Schütz-Bosbach, Endrass & Kathmann, 2012; Maeda, Kato, Muramatsu, Iwashita et al., 2012; Obhi, Swiderski & Farquhar, 2013; Voss, Moore, Hauser, Gallinat et al., 2010). These basic sensory-motor signals of control may serve as a critical reference for inferring control in more complex environments like the social domain, where optimal functioning and increased goal-directedness tends to be associated with those ranked closer to the top. If this is the case, we may observe some modulation via testosterone.

1.7.1. Brain mechanisms of the SoA

A large network of brain processes, spanning low-level sensory motor regions as well as top-down inferences and emotional factors have been shown to sustain and modulate the SoA (Moore & Obhi, 2012; Gentsch & Synofzik, 2014). In particular, it has been associated with brain regions such as the anterior insula (Farrer & Frith, 2002; Farrer et al., 2003; Sperduti, Delaveau, Fossati & Nadel, 2011), angular gyrus (Chambon, Wenke, Fleming, Prinz et al., 2012) pre-supplementary cortices (Kuhn, Brass & Haggard, 2013). Several theories have been put forward to explain how brain processes combine to engender feelings of agency. The ‘Comparator Model,’ which was developed by Frith et al. (2000) and Frith (2012) is based on the idea that goals or intentions are represented within the motor system in terms of the desired state that actions will produce. This then generates a motor command to produce movement and in turn leads to changes in sensory input (feedback). Motor commands are thought to be accompanied by an “efference copy” – an unconscious duplicate of the motor command which essentially is the predicted effects of motor output. More recently, it has been proposed that changes in interoceptive signals also form part of the predicted set of effects (Seth, Suzuki & Critchley, 2012). When there is consistency between external events and predictions made a priori about the effects of a voluntary action, the SoA then arises (Blakemore, Wolpert & Frith, 1998; Farrer et al., 2002; Haggard & Clark, 2003; Moore & Haggard, 2008; Wegner, 2002). Access to representations of how the pursuit and achievement of goals might affect not only the external environment but also one’s own internal milieu, is therefore integral to agentic experience.

More recent optimal cue integration theories (Moore and Fletcher, 2012; Synofzik, Vosgerau & Lindner, 2009) take account of the comparator model and align it with findings supporting an alternative explanation of the SoA – Wegner’s theory of apparent mental causation (Wegner & Wheatley, 1999; Wegner, 2002) in which the conscious intention to act and its associated observed outcomes are what lead to a sensation of agency. Moore and colleagues (2009) argue that both sensorimotor sources of information and external environmental cues contribute to the SoA but that these signals are weighted differently depending on the context. Specifically, it is the relative reliability of different signals at the time of action that determines their influence in the emergence of agency.

1.7.2. Agency and ‘knowing what you want’

It is not yet clear how, exactly, reliability in this weighting process is determined but there is some evidence to suggest that emotions and cues involved in decision-making may play a role. Ainley (2015) has shown that people with poorer ability to perceive internal bodily signals score lower on implicit measures of sensorimotor agency. This may interfere with getting a good “picture” of the predicted effects of actions and introduce conflict during decision-making, even if registered at the unconscious level. Conflict has in fact shown to be a moderating factor in the emergence of feelings of control. A study by Chambon et al. (2012) showed that internal processes that foster fluency at the time action selection are capable of increasing the SoA. This can even occur in situations where there is no real outcome (Wenke, Fleming & Haggard, 2010). For example, clues as to what the effects of a voluntary action will be, robustly enhance feelings of control, even when such effects and primes are unrelated to the action itself (Aarts, Custers & Wegner, 2005; Linser & Goschke, 2007; Sato, 2009). Such studies show that the predictability of action outcomes strongly influences the SoA and can do so *prospectively*. In other words, agency experiences can be illusory (Sato & Yasuda, 2005), based on sensory-motor cues that inform decision-making at the time of action preparation and may be strongly affected by what Guinote (2017) refers to in her studies of human social power as having a “strong agenda”. Indeed, illusory experiences of control have been associated with well-being and optimism (Perlmutter & Monty, 1977; Taylor & Brown, 1988) and are often described as the bedrock of a sense of omnipotence in powerful figures (Fast et al., 2009; Fast et al., 2012).

In fact, Karsh and Eitam (2015) found that feelings of control motivate behaviour in very similar ways to tangible rewards in the environment. That is, feeling in control is motivation in and of itself to pursue goals. This may explain how perseverance is maintained in spite of challenging circumstances. For instance, people who score higher on measures of implicit agency tend to have more optimistic attribution styles (Penton, Thiery & Davis, 2014). On the other hand, the anticipation of unpleasant outcomes has been shown to decrease the self-attribution of action (Yoshi & Haggard, 2013). This clear link between the SoA and approach motivation is supported by findings from Moore et al. (2010) who have shown that elevations in the neurotransmitter, dopamine, correspond with an increase in implicit experiences of sensory-motor control. The role of testosterone in reward processing (van Honk et al., 2004)

and testosterone's modulation of dopamine (Purves-Tyson, Owens, Double, Desai et al., 2014) suggests it may similarly impact the feeling of sensorimotor control.

1.7.3. Sense of agency in the social domain

Of relevance to social behaviour, one study demonstrated that individuals can experience pre-reflective feelings of agency over effects of their actions that are carried out by other social partners (Pfister, Obhi, Rieger & Wenke, 2014). The SoA may as such contribute in fundamental ways to the organization of social systems, where the actions of one individual very often constitute a coordinated effect of another's volitional behaviour. Mere position in a hierarchy and the decision-making privileges that this provides should influence agency since research has shown that simply having a choice to decide between actions appears to up-regulate agency (Barlas & Obhi, 2013). Obhi et al. (2012) have shown that by inducing people to feel socially powerless, implicit experiences of agency decline. In this way, sensorimotor signals of agency may help to constitute the phenomenology of power.

Thus, the "approach" motivation that characterizes powerful individuals (Guinote, 2017) and which is sustained to a large extent by the activity of testosterone (Terburg & van Honk, 2013) may derive in part from both a history of agentive experience that might manifest psychologically in terms of self-confidence and increased goal-directedness, but also spontaneously, while potential actions are being deliberated. This basic form of empowerment may not only contribute to the phenomenology of power, but it may also constitute an important self-deceptive and self-fulfilling mechanism by which dominance is initially achieved. The literature reviewed here suggests that basic sensory-motor processes that represent action-effect relationships may influence higher-order emotional experiences of control and power. However, no studies to date have formally explored a possible link between the brain's major neurochemical substrate of power and sensory-motor agency.

1.8. Literature overview

A large but steadily growing field, the literature on the social functions of testosterone highlights its central role in enhancing and preserving power by incentivizing the pursuit of reward (van Honk et al., 2004; Weber et al., 2017), downplaying the influence that others

have on goal-attainment (Bos et al., 20216; Wright et al., 2012) and by maintaining an implicit defensive stance in most social interactions (Bos et al., 2013; Terburg et al., 2012b; van Honk et al., 2001). However, questions remain as to how power is represented and regulated in the brain's more basic sensory-motor systems. This is in keeping with an embodied cognition framework in which bodily simulations are regarded as a constituting factor in mental and emotional experience (Barsalou, 2008). For instance, can we establish embodiment profiles for emotion states relating to territorial-type defensiveness, the enhancement of self-serving agendas and "approach" motivation?

Here I have proposed that representations of the body that function to guide action and gauge homeostasis provide an opportunity to further explore this question. If we take the body to be the locus of control, and consider that bodily representations of self and others define and influence the scope of action potentiality within the environment, testosterone should have demonstrable effects on the elementary processes that facilitate embodiment. These include, but are not limited to, interoceptive awareness, the experience of body ownership and the sense of agency. Indeed, this review has presented evidence which suggests that social variables are able to meaningfully interact with these sensory-motor processes, and vice-versa (Banakou, Grote & Slater, 2013; Durlík & Tsakiris, 2014; Izjerman et al., 2012; Maister et al., 2013; Moeini-Jazani et al., 2017; Paton et al., 2012; Pfister et al., 2014). The embodied cognition framework promises interesting new approaches to the study of low-level mechanisms that support the rise to power in terms of the basic experiences that bodily processes afford. However, as yet no studies have explored a potential role for hormones, and testosterone in particular, in the modulation of embodiment. The key objective of this dissertation is to address this gap in the literature.

1.9. Research questions

This dissertation comprises three studies in which the following research questions are explored:

Study 1. How does a single 0.5mg dosage of testosterone affect interoceptive accuracy at baseline and following a benign social threat? Does interoceptive accuracy correlate with indices of personality variables based on discrete, basic emotional systems?

Study 2. How does a single 0.5mg dosage of testosterone affect susceptibility to the Rubber Hand Illusion (RHI), an experimental procedure known to induce changes in body ownership? Do operational indices of the RHI correlate with subjective mood states?

Study 3. How does a single 0.5mg dosage of testosterone affect the implicit sense of sensory-motor agency, and is there any evidence that testosterone influences higher-order experiences of control as measured by optimism in affective forecasting?

1.10. Abstracts for experimental chapters

Chapter 2: The effects of testosterone on interoceptive accuracy.

Recently, several studies have demonstrated a link between interoceptive awareness, that is, accuracy in perceiving internal states of the visceral body, and resilience in socially stressful situations. These studies converge on the idea that interoceptive accuracy (IAcc) optimizes predictive models of the self in action, possibly relating to inferences of control. In the social sphere, control and resilience have consistently been linked to the steroid hormone, testosterone. However, whether testosterone has any effect on IAcc, particularly in situations that threaten control, remains unknown. In the present study, 49 females participated in a double-blind, placebo-controlled trial to test the effects of 0.5mg testosterone on IAcc, using a heartbeat tracking task. Testosterone improved performance in IAcc compared to the placebo group at baseline; however, this advantage was abolished following social ostracism in the online Cyberball game. These findings indicate that testosterone has the capacity to improve IAcc but that it may also facilitate iterative cycling between internally versus externally directed attention. Levels of IAcc appear to be state-like, with apparently adaptive social functions that are sensitive to social context.

Keywords: Interoceptive awareness; testosterone; power; control; embodied cognition.

Chapter 3: The territory of my body: Testosterone prevents limb cooling in the Rubber Hand Illusion.

The Rubber Hand Illusion (RHI) is an experimental paradigm for assessing changes in body ownership. Recent findings in the field suggest that social-emotional variables can influence such changes. Since body ownership is a mechanism that enables subjects to organise information about the environment and interact efficiently in it, changes in body ownership should have important implications for social power. In the current study, we investigated whether 0.5mg of testosterone, a steroid hormone strongly implicated in the achievement of power and dominance, affected the RHI. 48 females participated in a double-blind, placebo-controlled experiment in which the RHI was induced. Compared to placebo, testosterone had no effects on the usual induction of subjective ownership over the rubber limb or on proprioceptive drift. However, unlike the placebo group, testosterone-treated participants did not display an objective decline in the temperature of their own (hidden) hand following induction of the illusion. These findings suggest that testosterone strengthens implicit but not explicit bodily self-representations. We propose that effective maintenance of implicit body boundaries can be regarded, conceptually, as a primary defensive state facilitating integrity of the self.

Keywords: Testosterone; rubber hand illusion; body ownership; embodied cognition; limb temperature; social power; defence.

Chapter 4: Testosterone facilitates the sense of agency.

Sense of agency (SoA) refers to feelings of being in control of one's actions. Evidence suggests that SoA might contribute towards higher-order feelings of personal control – a key attribute of powerful individuals. Whether testosterone, a steroid hormone linked to power in dominance hierarchies, also influences the SoA is not yet established. In a repeated-measures design, 26 females participated in a double-blind, placebo-controlled trial to test the effects of 0.5mg testosterone on SoA, using an implicit measure based upon perceived shifts in time between a voluntary action and its outcome. Illusions of control, as operationalized by optimism in affective forecasting, were also assessed. Testosterone

increased action binding but there was no significant effect on tone binding. Affective forecasting was found to be significantly more positive on testosterone. SoA and optimistic expectations are basic manifestations of power which may contribute to feelings of infallibility often associated with dominance and testosterone.

Keywords: Sense of agency; testosterone; control; mood; affective forecasting; optimism; embodied cognition.

Chapter 2 | Experiment One: The effects of testosterone on interoceptive accuracy

2.1. Introduction

Testosterone is an anabolic hormone which has been closely linked to parameters of physical power and performance in both males and females (Anawelt & Merriam, 2001; Bhasin et al., 1996). Aside from these physiological functions, the benefits of testosterone extend into the social domain (van der Westhuizen & Solms, 2015). Considerable research demonstrates a central role for the hormone in achieving social control by monitoring threat and increasing competitive social motivation. Several studies show that testosterone improves tolerance for risk (Apicella et al., 2008; Ronay & von Hippel, 2010; Stanton, Liening & Schultheiss, 2011) and reduces fearfulness (Bos et al., 2013; van Honk et al., 2005). At the same time, testosterone has been shown to increase vigilance to cues of social threat (Terberg et al., 2012) yet encourage fairness in bargaining games (Boksem et al., 2013; Eisenegger et al., 2010) while simultaneously reducing certain empathic abilities such as “mind reading”, automatic mimicry and the ability to effectively collaborate with others (Hermans et al., 2006; Montoya et al., 2012; van Honk et al., 2011; Wright et al., 2012). Thus, existing research suggests that testosterone appears to promote an “inward” mentality and a wide repertoire of emotional processes and behaviours aimed at maintaining control but no studies to date have explored whether these effects can be further explained by embodied mechanisms.

From the perspective of embodied cognition (Barsalou, 2008; Lackoff, 2012; Varela et al., 1992), in which basic sensory-motor processes are regarded as integral to mental representations, the state of the body and the way in which this information is processed by the brain should serve as a reference for inferences about control. For example, independent of its physiological effects, the advantages of testosterone to competitive performance have been suggested to emerge from improved signalling of effort or the “readiness to perform” (Cook & Beaven, 2013). An important source of this kind of information, increasingly recognised for its role in social cognition and emotion, are interoceptive signals from the body (Fotopoulou & Tsakiris, 2017), which are integrated in the insula cortex (Craig; 2002; Craig, 2009). The term ‘interoceptive awareness’ describes these internal feelings which

provide a sense of the body's current condition (Cameron, 2001; Craig, 2002). On objective testing, this ability is referred to as 'interoceptive accuracy' (IAcc) (Garfinkel et al., 2015).

Several studies provide support for the idea that accuracy in detecting visceral signals from the body (IAcc) informs a sense of control by facilitating pro-active decision-making, particularly those relevant to the self, and by increasing tolerance for negative affect. Though a great deal of past research links high IAcc to anxiety (Domschke et al., 2010), recent findings show that IAcc is elevated in individuals with a higher dispositional sense of social power (Moeini-Jazani et al., 2017). In fact, by increasing social control, studies report a corresponding increase in IAcc (Kuntsman, Clerkin, Palmer & Peters, 2016; Moeini-Jazani et al., 2017). This kind of attention to internal sensation appears to play an integral role in adapting to socially challenging situations (Füstos et al., 2012; Haas et al., 2016; Herbert, Ulbrich & Schandry, 2007; Pollatos, Matthias & Keller, 2015; Werner et al., 2009; Werner et al., 2013). For instance, using a heartbeat-tracking task, a commonly used procedure for assessing interoception (Schandry, 1981), Werner et al. (2009) found that better IAcc was associated with less anxiety before and after a public speaking performance. Similarly, indices of enhanced interoceptive processing have been linked to higher resilience (Haas et al., 2016), less worrying about body sensations (Baranauskas, Grabauskaitė & Griškova-Bulanova, 2017) and more reliance on "gut" feelings during emotional decision-making (Dunn et al., 2010). Individuals with high IAcc are also known to cope better in response to social ostracism – Pollatos et al. (2015) found that social exclusion in an online cyber-ball paradigm caused less emotional distress in individuals with high IAcc, who were also more likely to re-affiliate.

The role of IAcc in predicting and evaluating the affective consequences of one's own motivated action (Brass & Haggard, 2010) may explain these findings. For instance, variation in IAcc relates to internal predictive models of sensory self-monitoring (Critchley, 2005) as well as the ability to accurately predict and appraise threats to homeostasis (Canon, 1929; Grillon, Baas, Lissek, Smith, et al., 2004; Nelson, Kessel, Jackson & Hajcak, 2015; Paulus et al., 2009; Pezzulo, Rigoli & Friston, 2015). Error signalling in the brain is known to be more prominent in people with anxiety and avoidance-related psychopathologies (Hajcak & Foti, 2008; Moser, Moran, Schroder, Donnellan et al., 2013; Paulus & Stein, 2006; Weinberg, Olvet & Hajcak, 2010), possibly because errors in predictive processing activate the same brain regions that give rise to negative affect and 'loss' in general

(Eisenberger, Jarcho, Lieberman & Naliboff, 2006; Foti, Weinberg, Bernat & Proudfit, 2015; Spunt, Lieberman, Cohen & Eisenberger, 2012). Error signalling can be interpreted within a Bayesian or probabilistic formulation of mental experience, where the brain is regarded as a statistical organ that forges generative models of the environment to minimize predication error (Friston, 2010, Friston et al., 2009, Gregory, 1980, Helmholtz, 1866), i.e., the difference between top-down expectations and current sensory feedback.

Thus, in general, the literature suggests that individuals with more accurate interoceptive awareness are better able to model their embodied environment (Tsakiris, Tajadura-Jiménez & Constantini, 2011). Accurate predictions of volitional effort may serve as an important proxy for guiding approach motivation since errors in interoception appear to be experienced as threatening – as *loss* – with concomitant feelings of uncertainty (Gray, Harrison, Wien & Critchley, 2007; Picard & Friston, 2014; Sarinopoulos, Grupe & Mackiewicz, 2010). More precise predictive modelling may free up cognitive capacities to efficiently attend to problems (Paulus & Stein, 2006; Werner et al., 2013). From this perspective, lower IAcc may undermine social power by drawing attention outwards and by disrupting efficiency of processing to impinge on approach motivation. This is in agreement with Pollatos, Matthias and Keller's (2015) recent proposal that faster or more differentiated recognition of changes in bodily reactions “might help to constitute a feeling of higher control over one's negative experiences in everyday life” (p.786). If IAcc does indeed contribute to this capacity, given the links between testosterone and social power, we should expect a demonstrable effect of testosterone on interoceptive processing.

2.1.1 Testosterone and interoceptive processing

Indirect evidence links testosterone to improved IAcc. Firstly, males compared to females tend to show superior interoceptive performance on heartbeat tracking tasks (Harver, Katkin, & Bloch, 1993; Grabauskaite, Baranauskas & Griškova-Bulanova, 2016; Katkin, Blascovich, & Goldband, 1981; Roberts & Pennebaker, 1995) and estimates of blood glucose levels (Cox et al., 1985). These differences suggest a role for testosterone – the hormone with among the largest difference between the sexes. It is possible, however, that female's poorer performance is mediated by other factors, such as higher on-average BMI (Herbert & Pollatos, 2014), or lower blood pressure (Kienitz & Quinkler, 2008), which has been correlated positively with IAcc (Koroboki et al., 2010). However, one study found that,

at least in children, superior performance in boys was not mediated by lower BMI (Koch & Pollatos, 2014).

Testosterone's activation of and affinity for the insula (Banczerowski et al., 2001; Bos et al., 2010; Heany et al., 2015; Lentini et al., 2013) provides compelling evidence for its role in interoception. A recent study in trans-gender men demonstrated that long term testosterone treatment not only increased cortical thickness in the insula, but also resulted in greater connectivity in brain regions associated with self-referential processing and own-body awareness (Burke et al., 2017). These findings may shed light on the role of testosterone in representing physical effort and the readiness to act (Cook & Beaven, 2013).

Aside from its role in integrating interoceptive information, the insula has been strongly linked to risk-assessment and the processing of threat (Bossaerts, 2010; Preuschoff, Quartz, & Bossaerts, 2008; Wiech, Lin, Brodersen, Bingel et al., 2010). Studies show that testosterone facilitates similar functions, promoting vigilance to social threat in ways that facilitate approach (Terburg et al., 2012; Radke et al., 2015). Mimicking the effect of testosterone on bargaining (Burnham, 2007; Mehta & Beer, 2010), increased insula activation is related to rejection of unfair offers in the Ultimatum Game (Sanfey et al., 2003) and individuals with high interoceptive abilities tend to be more averse to loss (Sokol-Hessner et al., 2014). Though testosterone has traditionally been thought to promote impulsiveness, a form of recklessness –this appears to depend on high cortisol levels (Montoya et al., 2012; Terburg & van Honk, 2009). Recent findings indicate that it in fact significantly reduces risky, cold bluffing in Poker games when status disputes require less adventurous and more conservative behaviours (van Honk et al., 2016). Indeed, at the heart of competitiveness is the aversion to *loss*. Interoceptive processes may therefore interact with testosterone to monitor loss and thereby regulate competitive motivation.

2.1.2. Aims

Against this background, this study investigated the effects of 0.5mg testosterone on IAcc in a female sample, as measured by a heartbeat-tracking task. In line with the hypothesis that interoceptive processing may facilitate “approach” behaviour, we predicted that testosterone would significantly increase baseline IAcc relative to placebo. Given that changes in interoception may in turn help to monitor loss, to investigate the effects of testosterone on

bodily awareness in response to social threat, we assessed changes in IAcc following ostracism in an online Cyber-ball game. Rejection in this game has been shown to reduce circulating levels of testosterone in both men and women (Radke et al., 2017; Seidel et al., 2013).

2.2 Methods

Ethical approval was granted by the University of Cape Town's (UCT) Human Research Ethics committee (HREC REF 868/2014). All data was collected in accordance with the Declaration of Helsinki. Informed consent was obtained prior to commencement of the study and debriefing took place upon completion of data collection. There were no reports of negative side effects from the testosterone or placebo administration and no participant withdrew from the study.

2.2.1. Participants

49 right-handed female participants, aged between 18 and 30 years and from varying cultural and ethnic backgrounds within South Africa, were recruited to participate in the study in exchange for 18 USD. Testing was performed during the pre-ovulatory phase of the menstrual cycle since androgen levels are relatively constant during this time. Individuals who were taking any form of hormonal contraception or other medication were excluded, as were those with a history of psychiatric illness or a BMI over 30.

2.2.2. Materials and Measures

2.2.2.1. Heartbeat tracking device

Following Tsakiris et al., (2011), IAcc was measured with a mental heart-beat tracking task (Schandry, 1981). An optical heart rate sensor ("Pulse Sensor"; pulsesensor.com) was placed on the index finger of the left hand. The sensor was connected to a data acquisition unit (NI-USB 6000, National Instruments, NI) that sampled at 1 kHz. The corresponding arterial pulse waveform was recorded by a custom-written computer program that also implemented the heart-beat tracking task (Elemedic; www.elemedic.com), implemented using LabView

(NI) software.

This investigation into heartbeat tracking accuracy was the first of its kind at the University of Cape Town, and South Africa at large. We therefore collaborated with our colleagues from UCT's Biomedical Engineering Department to develop the experimental device and ran a pilot study to validate its measurement.

2.2.2.2. Cyberball Social Ostracism Task

The Cyberball task is a simple computerised game that was developed by Williams, Cheung and Choi (2000). We developed a version of the software in collaboration with colleagues from UCT's computer science department. It is played by the participant and two avatars, and consists of 30 ball tosses between the three players. To increase ecological validity, a profile picture of the participant was taken prior to the experiment and they were told that this would be uploaded next to their avatar for the other players to see even though it would not be visible to them. Photographs of the 'other players' were accessed from an online database and matched for race. In the ostracism condition, participants receive the ball twice at the very beginning of the game and are then excluded from the ball-tossing from that point onwards. This game is a valid manipulation of social in-group status (Eisenberger et al., 2006; Hawkey, Williams & Cacioppo, 2011; Williams & Jarvis, 2006) and rejection in Cyberball has been linked to reduced feelings of belongingness, self-esteem, and personal control as well as increased sadness and anger (Sebastian et al., 2010).

2.2.2.3. Post-Cyberball Questionnaire

The Post Cyberball Social Ostracism Questionnaire is a manipulation check utilised in several previous studies to assess emotional reactions to the task (Durlak & Tsakiris, 2015; Williams et al., 2002). Participants are asked to rate on a 5-point scale the extent to which they agree with statements assessing positive and negative affect (4 items each, score out of 20) and four fundamental social needs: belonging, control, meaningful existence and self-esteem (3 items each, score out of 15). The questionnaire has additional items that gauge whether or not the participant recognised their ostracised status (2 item, score out of 10).

2.2.2.4. Personality Measures

Prior to the experimental session, participants completed the Affective Neuroscience Personality Scales (ANPS). The ANPS (Davis & Panksepp, 2011; Davis, Panksepp & Normansell, 2003) was designed to measure the relative influence on personality of six ‘basic emotion’ systems, namely PLAY, SEEKING, CARE, FEAR, RAGE and PANIC/GRIEF. Van der Westhuizen and Solms (2015) developed a revised version of this scale to include the basic emotion, LUST, and to assess whether trait dominance can be considered a distinct dimension of emotional functioning. This revised version was utilised in the current research.

Positive traits in particular have implications for emotion regulation and social interaction (Burgdorf & Panksepp, 2006) and were thus included in the study to examine how they may relate to IAcc. Negative emotions, like RAGE, for example, are indicative of the tendency toward emotional dysregulation. The initial development of these scales was driven by speculation that they might form the affective basis of the widely endorsed Five Factor Model (FFM) of personality. Indeed, high correlations between the two models have been reported (Davis et al., 2003). Each subscale in the ANPS consists of 14 items in the form of statements designed to represent the basic emotions. Respondents report the extent to which each item describes their personality. The ANPS has good psychometric properties (Davis et al., 2003) and has been validated by clinical researchers (Reuter, Panksepp & Schnabel, 2005; Savitz, van der Merwe, & Ramesar, 2008). Furthermore, in the revised version, the salivary testosterone: cortisol ratio was uniquely associated with trait dominance, lending credibility to the construct (van der Westhuizen & Solms, 2015).

2.2.3. Procedure

Participants were assigned to a testing schedule in which group allocation (testosterone versus placebo) was randomized to ensure equivalent groups. Codes were assigned for anonymity. Each participant was tested on one occasion in a double-blind, between-subjects design in which neither researcher nor participant had knowledge of group assignment. During piloting, we discovered that participants were intrigued by the heartbeat tracking task, especially if their accuracy was low, and thus, a post-test only design was favoured over a pre-test – post-test design to prevent any possible practice effects that might be incurred during the several hour interval between administration and testing. Indeed, Weisz,

Balazs & Adams (1988) report a learning effect of heartbeat tracking in a repeated-measures design (and see also Marshall & Epstein, 1978).

To control for hormonal fluctuations in diurnal cycles, testing sessions were standardised to the afternoon. Males were excluded because the time course of effects in the current testosterone administration protocol have only been reliably established in women and formal establishment in men is unfeasible (Tuiten, Van honk, Koppeschaar, Bernaards et al., 2000). Testing was performed during the pre-ovulatory phase of the menstrual cycle since androgen levels are relatively constant during this time (Nieschlag, Behre & Nieschlag, 2012). Participants were supplied with a calendar to track their cycles and phase was confirmed the day before testing. Participants reported to the lab exactly 4 hours prior to the experimental session at which time they completed the ANPS and received sublingual administration of testosterone or placebo. This schedule was based on previous research which has shown the efficacy of sublingual testosterone administration to peak 4-6 hours later (Tuiten et al., 2000) and has been repeated in many subsequent testosterone administration studies (Terburg, Aarts & van Honk, 2012b; Terburg et al., 2016; van Honk et al., 2001, 2011, 2016). The sample was comprised of 0.5mg of testosterone, 5mg of the carrier hydroxypropyl beta cyclodextrin, 5mg ethanol and 5ml of water. For the placebo samples, the testosterone was omitted. Both samples were identical to taste.

During the interval, participants were requested to refrain from engaging in strenuous or sexual activity, to avoid consuming excessive caffeine, to refrain from smoking and eating during the one hour prior to the experiment.

After providing a general overview of the experiment, participants were seated in front of a computer screen and connected to the pulse sensor. Their hands rested in parallel on the table in front of them and they were instructed to uncross their legs. Each participant was told that they would need to concentrate and try to count their heart beat, without moving or touching any part of their body. This process was described as trying to “listen” or “feel” for each heart beat. Instructions were given both verbally by the researcher and visually on the computer screen.

At the start of each trial, participants saw the word “Go” on the screen in front of them which was accompanied by an audio tone. The trial ended with the word “Stop” and another audio tone. There was a single training interval of 10 seconds, followed by three test intervals. Test

intervals of 45, 35 and 30 seconds were counterbalanced across participants. At the end of each trial, the participant verbally reported their heartbeat count, which was compared with the objective wave-forms counted manually after the experiment. No feedback on the participant's performance was given.

In keeping with standard practice (Durlak & Tsakiris, 2015; Pollatos et al., 2012; Werner et al., 2013), IAcc scores were calculated according to the following formula, which yields a score ranging from 0-1:

$$1/3 \sum (1 - (| \text{actual heartbeats} - \text{reported heartbeats} |) / \text{actual heartbeats})$$

After obtaining this baseline measure of IAcc, participants took part in an online Cyberball game where they were systematically ostracised. They were told that they would be playing with other participants who were signed onto the network from another location. Within one minute following the cessation of Cyberball, the heart-beat tracking task was administered for the second time. Participants were then administered the Post Cyberball Social Ostracism Questionnaire.

Before leaving, BMI was calculated by recording the height and weight of each participant. Because heart-rate has been shown to mediate IAcc scores (Knapp-Kline & Kline, 2005), a measure of heart-rate was determined by calculating beats per minute based on the objective counts of each trial in the heart-beat tracking task. All data was recorded into excel spread sheets and later coded into SPSS version 22.0 (SPSS, IBM. Corporation, 2013, Chicago, IL.) for analysis.

2.3. Results

Prior to the analyses, the data was screened for outliers and then tested for violations of the assumptions required for the use of standard parametric analyses. No outliers were found but the data did not uphold the assumption of normal distribution. Refer to Table 2.1 for a summary of descriptive statistics for the IAcc scores of the placebo and testosterone groups. Note that "IAcc-change" refers to the difference between baseline and post-Cyberball IAcc scores. This variable conveys the magnitude and direction of IAcc change in response to the Cyberball social ostracism task.

Heart-rate (HR) during the heart-beat tracking task at both baseline ($t(47) = 0.26, p = .97$) and post-Cyberball ($t(46) = 0.023, p = .98$) did not differ by group. Mean HR in the testosterone group was 72.61 (SD = 9.98) at baseline and 71.55 (SD=10.69) post Cyberball. The mean HR for the placebo group was 72.71 (SD=11.36) at baseline and 71.62 (SD=9.71) after Cyberball. IAcc at baseline did not correlate with heart-rate ($r = -.32, p > .05$).

Table 2.1

Summary of the descriptive statistics of the placebo and testosterone groups

Measure	Placebo		Testosterone	
	<i>n</i>	<i>M</i> (SD)	<i>n</i>	<i>M</i> (SD)
Baseline IAcc	27	.62 (.22)	22	.76 (.17)
IAcc Change	26	.04 (.15)	22	-.08 (.18)

Results from a Mann-Whitney U-test confirmed that the testosterone group were significantly more accurate in the heartbeat tracking task than placebo at baseline ($U = 196, z = -2.030, p = .042, r = -.29$), by approximately 14%. There were no significant differences between the groups on IAcc scores after Cyberball.

Because we were interested in the direction of change in interoceptive accuracy between groups in response to ostracism, we next investigated the difference between placebo and testosterone groups in terms of the change in IAcc following rejection in the Cyberball game. Based on a Mann-Whitney U-test, the change in IAcc from baseline to post-cyber ball differed significantly between placebo and testosterone ($U = 181, z = -2.173, p = .030; r = -.31$). IAcc in the testosterone group was reduced from .76 to .68, which is roughly comparable to baseline values of the placebo group. In contrast, the placebo group increased from .62 to .66 following Cyberball. Wilcoxon Signed Ranks tests showed that this change approached significance for the testosterone group ($z = -1.61, p = .054, r = -.34$), but not for the placebo group ($z = -1.07, p = .14, r = -.21$).

Results from the Post Cyberball Questionnaire were compromised by several missing data points but results from the sample of 42 indicated that there were no significant differences between placebo and testosterone groups on measures of affect, ostracism status, feelings of belonging, control, meaningful existence or self-esteem. Statistics are displayed in Table 2.2.

Scores out of a total of 10 for “ostracism status” indicate that both groups recognised that they were being excluded from the ball tossing game. It was not possible to contrast reactions to rejection with social inclusion since all participants were ostracised, however, a one-tailed t-test showed a trend toward negative mood scores being significantly higher than positive mood ratings, $t(40) = -1.652, p = .052$. We can therefore conclude that our manipulation was successful in eliciting the experience of social ostracism.

Table 2.2

Descriptive statistics for the post Cyberball questionnaire

	Placebo (n = 22)	Testosterone (n = 20)	<i>t</i>	<i>p</i>
Positive Affect	9.00 (3.26)	9.45 (3.25)	-.45	.66
Negative Affect	10.55 (3.94)	10.55 (3.44)	0	1
Meaningful Existence	11.05 (3.57)	12.00 (3.49)	-.85	.40
Belonging	7.85 (3.70)	6.10 (2.35)	1.78	.08
Self-esteem	9.55 (2.52)	8.55 (1.93)	1.47	.15
Sense of Control	4.05 (1.43)	3.80 (1.79)	.49	.63
Ostracism Status	8.80 (2.16)	8.65 (2.20)	.22	.83

Relationships between personality variables and scores on the heart-beat tracking task were examined testosterone. One outlier of more than 3 SDs from the mean was removed from the ANPS. Refer to Table 2.3 for a summary of correlations. Baseline IAcc was significantly negatively correlated with scores on the ANGER and LUST subscales of the ANPS. However, after applying a Bonferonni correction which specified alpha at .008, only the ANGER finding remained significant. This means that people low in IAcc tended to score higher on measures of ANGER. No other significant correlations were observed.

Table 2.3.

Correlations between measures of interoceptive accuracy and the Affective Neuroscience Personality Scales

	SEEKING		FEAR		CARING		ANGER		PLAY		SADNESS		LUST		DOM.	
	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>
Baseline	-.04	(.84)	-.17	(.33)	.10	(.58)	-.47	(.005)	-.14	(.43.)	-.18	(.32)	-.50	(.03)	-.22	(.21)
IAcc																
IAcc	-.03	(.87)	-.01	(.97)	.03	(.86)	.13	(.47)	.03	(.86)	.19	(.27)	.15	(.39)	.13	(.46)
Change																

N = 48; DOM = Dominance.

2.4. Discussion

Based on the hypothesis that elevated levels of testosterone facilitate IAcc to support coping and decision-making in stressful social situations, this study aimed to investigate the effects of 0.5mg of testosterone compared to placebo on a heartbeat-tracking task in a sample of females. Testosterone significantly increased IAcc at baseline. However, this advantage was abolished following ostracism in an online game. To the best of our knowledge, this study is the first to experimentally probe the effects of testosterone on interoceptive processing.

2.4.1. Testosterone elevates baseline IAcc

On average, the testosterone group was 14% more accurate in perceiving their heartbeats than the placebo group. The improved interoceptive accuracy at baseline demonstrated by the testosterone group may explain why individuals with generally high levels of the hormone tend to be socially dominant and cope more proactively in socially stressful situations. Affirming this link between interoception and control, Moeni-Jazani et al., (2017) recently showed that participants placed in positions of power outperformed their subordinate counterparts in a heart-beat tracking task. As a trait, high IAcc has been linked to greater resilience during times of social stress, possibly by way of improved predictive models of sensory self-monitoring (Brass & Haggard, 2010; Tsakiris, Tajadura-Jiménez & Constantini, 2011). For instance, problems in predicting the consequences of action sequences and using those predictions to drive goal-directed decision-making have been implicated in the reduction of behavioural engagement and output (Cortlett et al., 2011;

Heerey & Gold, 2007). It is therefore plausible that the social approach orientation characteristic of people with high baseline levels of testosterone is mediated, at least in part, by self-focus and an increased sense of certainty in decision-making, presumably afforded by elevated IAcc (Moeini-Jazani et al., 2017; Picard & Friston, 2014; Werner et al., 2013). This is in line with Pollatos et al. (2015) who have suggested that the ability to differentiate changes in bodily responses might contribute to a feeling of increased control over negative experiences. In accordance, trait ANGER, a personality variable characterised by unbridled feelings of frustration, correlated negatively with baseline IAcc.

When testosterone levels are high, improved IAcc may help to signal the adequacy of bodily resources. For instance, Ainley and Tsakiris (2013) found that IAcc is positively related to feelings of bodily competence and Baranauskas et al. 2017 found heartbeat evoked potentials to be inversely related to worries about body sensations. Furthermore, both force and effort sense have previously been related to activity in the insula (de Graaf et al., 2004; Williamson, McColl, Mathews, Ginsburg, & Mitchell, 1999), a major brain substrate of interoceptive processing (Craig, 2009). Given the effect of testosterone on physical strength (Bhasin et al., 1996), our findings suggest that the relationship between body competence and IAcc could function in the opposite direction as well. That is, feelings of physiological competence may improve interoceptive accuracy by increasing precision-weighting of interoceptive priors. According to Ainley et al. (2016), accurate detection of heart beats requires a prior belief about the importance of one's own internal sensations. Thus, when asked to keep count of heart beats, attention can be used effectively within the interoceptive system to raise the precision of predictive errors relative to priors. Elevated IAcc at baseline suggests that testosterone may play a role in this regard. This perspective is supported by Cook and Beaven's (2013) finding that testosterone appears to influence motivation by signalling the body's readiness to act. We propose that the improved IAcc displayed by the testosterone group may promote a sense of control, which manifests firstly in the bodily domain but then extends to the conceptual domain as information is registered in the brain and begins to associate hierarchically (Critchley & Garfinkel, 2018; Maister et al., 2014). Because we did not measure the effects of testosterone on changes in bodily phenomenology, future studies will be needed to investigate this proposed mechanism.

In the absence of other bodily cues signalling competence (Krauss-Whibourne, 2012), enhanced IAcc may promote the kind of vigilance that is more closely associated with social

anxiety and less with vigilance related to testosterone and social status motivations (Terberg et al., 2012). This may explain why several studies demonstrate a positive relationship between IAcc and panic or anxiety (Domschke et al., 2010; Dunn et al., 2010; Pollatos et al., 2007). Such distinctions suggest that the detection of interoceptive signals may be influenced by several divergent channels in line with Bayesian formulations (Friston, 2010).

It is important to consider that because resilient, positively-valenced personality styles (Seeking / Dominance) did not predict improved interoceptive ability, it is possible that higher baseline IAcc in the testosterone group may simply reflect peripheral changes in the body. Testosterone is thought to be a major factor in hypertension (Kienitz & Quinkler, 2008) and one study found that increased blood pressure transiently increased accuracy in detecting heart rate (Koroboki et al., 2010), raising the possibility of peripheral action. Unfortunately, we did not measure blood pressure and can therefore only speculate on these possibilities. However, because other studies have shown no effect on blood pressure in response to status-threats (Newman, Sellers & Josephs, 2005), the observation of a decline in IAcc following Cyberball rejection in the testosterone sample casts doubt on the mediatory role of blood pressure in initial elevation. Nonetheless, it is possible, furthermore, that the effects of testosterone on baseline IAcc may be explained by enhanced physiological arousal and heart rate contractibility. For instance, Van Honk et al. (2001) have previously shown that testosterone accelerates heart rate in response to angry faces. It may be that heart rate increased from pre-administration to post-administration of testosterone and that such changes had the effect of attracting attention to heart contractions. We did not track changes in heart rate in this way and can therefore only speculate. However, this interpretation is not supported by the current data set since we observed no differences in heart rate between the testosterone and placebo groups, nor any changes in the testosterone group from baseline to post-Cyberball despite changes in IAcc. Most notably, previous studies show no effect of testosterone on heart rate in the absence of hostile emotional stimuli (van Honk et al., 2001), suggesting that a notable change from pre to post administration of the hormone was unlikely.

Neuroanatomical studies provide some evidence for a central brain mechanism in the modulation of IAcc (Critchley et al., 2003; Pollatos et al., 2007) by testosterone. The findings presented here are consistent with data from imaging studies showing activation of the insula cortex by testosterone (Bos et al., 2010; Lentini et al., 2013) and increased gray matter

volume in the operculum and somatosensory cortices related to fetal testosterone level (Lombardo et al., 2012). These brain regions are known to be recruited during interoceptive processing (Craig, 2003; Critchley, 2004). Testosterone has also been found to restore arginine vasopressin innervation of the nucleus of the solitary tract (NST; Goudsmit, Fliers & Swaab, 1988), a key structure of the brain's interoceptive system receiving afferent input from the body periphery (Craig, 2003) and which shows considerable androgenic immunoreactivity (Hamson, Jones & Watson, 2004). These findings suggest that the effect of testosterone on IAcc may be centrally mediated.

2.4.2. Reactions to Cyberball

Based on findings from Durlak and Tsakiris (2015) who report a drop in IAcc following rejection in the Cyberball game, we expected a decline in heartbeat tracking accuracy in response to ostracism in the placebo group. However, in contrast to Durlak and Tsakiris (2015) we found no such decline in IAcc in the placebo group. Instead, we report a significant drop in the participants administered testosterone only, even though mood ratings across the two different groups were equivalent. One possible explanation for this disparity in the placebo group compared to Durlak and Taskiris (2015) may be attributed to differences in the participant populations. The legacy of apartheid in South Africa has meant that many groups experience racial and cultural discrimination on a daily basis (Seekings, 2008). Despite the fact that participants were matched for ethnicity in the Cyberball game, recurrent social threat in daily life may increase the threshold at which emotional responses are elicited through a process of habituation (Dijksterhuis & Smith, 2002). The subtlety of the Cyberball task may be less effective in eliciting a pronounced reaction from members of the South African population compared to those from Europe.

Consistent with previous findings that declining IAcc associates with the experience of rejection (Durlak & Tsakiris, 2015; Pollatos et al., 2015), the relative drop in IAcc in those individuals administered testosterone and who previously displayed higher IAcc, could be taken to suggest that they, specifically, were sensitised to the ostracism manipulation. This may explain why, despite expected drops in testosterone levels in both groups following rejection (Seidel et al., 2013), only the treatment group showed poorer performance on a second measure of the heartbeat tracking task. The finding here suggests that the testosterone group experienced dysregulation following this type of social threat. In keeping with this

view, previous research has shown that people who are more accurate in detecting their internal bodily signals tend to be more averse to loss, but importantly, in ways unrelated to risk aversion (Sokol-Hessner et al., 2015). The embodied reaction to social rejection displayed by the testosterone-treated group is consistent with studies showing that high testosterone individuals reject unfair offers in economic bargaining games (Burnham, 2007) and that testosterone increases vigilance to socially threatening cues (Hermans, Ramsey & van Honk, 2008; van Honk et al., 1999; van Honk et al., 2000; Wirth & Schultheiss, 2007) and drives competitive defensiveness (Booth et al., 2006; Eisenegger et al., 2016). This aligns with the widely endorsed idea that the role of testosterone in social behaviour has to do with achieving high status and preventing its loss (Eisenegger et al., 2011).

Although it could be argued that a decline in bodily awareness is fundamentally disempowering (Moenin-Jazani et al., 2017), that testosterone discourages “approach” responses in reaction to unfair social treatment (Burnham, 2007) is consistent with a decline in IAcc and evidence suggesting that higher acuity is instead linked to proactive reactions like reappraisal (Füstös et al., 2012). It may be that a transient change in interoceptive processing has the effect of signalling a loss and that high baseline IAcc is necessary for detecting these changes and providing the motivational impetus to react accordingly. For example, Lenggenhager et al. (2013) have argued that amplified feedback of one’s own visceral processes increases a self-centred perspective, leading to greater feelings of unfairness when mistreated and higher likelihood of retaliation. Transient feelings of a loss in bodily information might possibly explain the elevated defensiveness in response to status violations that characterises high testosterone individuals.

An effect of testosterone on IAcc following ostracism is, however, not consistent with the data from the post-Cyberball questionnaire. We did not find any significant differences in affect or attitude between placebo and testosterone groups following exclusion in the Cyberball game. Nonetheless, these findings are in correspondence with previous research showing that participants administered testosterone fail to reliably report any changes in affect (Eisenegger et al., 2010). This suggests that testosterone influences behaviour and perception implicitly, and indeed van Honk, Peper & Schutter (2005) have found this to be the case. Though interoception, in its very definition, is a form of sensation (Craig, 2003) the impact that it has on emotional state and performance is likely to be implicit. For instance, while an individual may have conscious access to their heartbeat, they may be unaware of

how this information affects confidence in decision-making. Feelings related to control may not show up in taxonomies based on reports of basic emotions (Ekman & Rosenberg, 1997; Panksepp, 1998), but from an embodied cognition perspective, access to bodily or “gut feelings” and the fluency of cognitive operations appear to impinge on emotions (Dunn et al., 2010; Pollatos et al., 2015).

In the model proposed based on the findings here, competitiveness could be understood as an implicit aversion to loss and social loss may be understood similarly to physiological loss (Ijzerman et al., 2012). High trait IAcc may not simply relate to empowerment *per se*, but enable a sense of control that derives from adeptness at recognising cues to potential loss of power in its various guise. Those in control may perceive themselves as having more to lose and seek sensory information to confirm this belief. From a Bayesian active inference perspective (Pezzulo, Rigoli & Friston, 2015), when testosterone is high and status becomes uncertain, sensory evidence relating to one’s state of control would capture attention, raising the precision-weighting of errors related to these social cues. Under conditions of status violation, these externally derived cues may take precedence over the precision of internal signals, explaining a drop in IAcc.

Consistent with this perspective, Durlak and Tsakiris (2015) propose that a decrease in IAcc following a status-threatening encounter is due to the allocation of cognitive resources away from the individual’s current internal state and toward relevant factors in the environment. In other words, the drop in IAcc may be indicative of a switch from the proactive to the reactive control system (Tops et al., 2010). The proactive control system is a noradrenalin-fuelled network associated with the posterior dorsomedial cortex, which guides behaviour in familiar settings on the basis of internally-directed, context models (i.e., priors) of self and others. The reactive control system, on the other hand, is more closely related to the ventral pathway and guides behaviour under conditions of rapid change and unpredictability.

A mediatory role for the reactive system in reducing IAcc is supported by the findings that testosterone increases reactive aggression to provocation (Denson & Mehta, 2013; Pope, Kouri & Hudson, 2000; Räsänen et al., 1999). Social rejection may be perceived by those high in testosterone as a provocation. Consistent with this interpretation, in our placebo sample, we found a negative correlation between baseline IAcc and trait anger, which is indicative of a reactive emotional style (van der Westhuizen & Solms, 2015b).

There is, however, no consensus on the exact contribution of interoceptive awareness to social cognition. We cannot, therefore, exclude the possibility that our finding of a relative decline in IAcc in the testosterone group following social ostracism reflects instead a mechanism for re-affiliation and the restoration of social status. Such a response would be consistent with the literature showing that testosterone promotes pro-social behaviour when such a response serves status seeking (Boksem et al., 2013; Eisenegger et al., 2010). Rejection in the online ball tossing game is a relatively benign form of social threat and lacks a competitive element that might justify an offensive response. In accordance with the ideas put forward by Quattrocki and Friston (2014), that an appropriate empathic response may require the suppression of interoceptive signals to facilitate the processing of an other's autonomic cues, the decline in IAcc may facilitate a strategy aimed at social reintegration. This interpretation is consistent with Fotopolou and Tsakiris' (2017) suggestion that "good-enough" IAcc is sufficient for social cognition. Although we did not give participants any further opportunity for social interaction with the other Cyberball players, Pollatos et. al (2015) found that individuals with higher IAcc were more likely to pursue avenues for behavioural affiliation in response to ostracism. A replication study that is able to assess attitudes and decision-making, not only in response to ostracism but in more hostile, competitive contexts too, is needed to further explore the functional significance of testosterone on IAcc.

2.4.3. Limitations

The current findings should be considered with the following limitations in mind. The sample size used here for a between-subjects design was relatively small. A within-subjects design will yield more statistical power to explain some of the discrepancies observed here, such why resilient personality styles were not predictive of IAcc. Indeed, a noteworthy shortcoming of the current study relates to its design. However, a pre test-post test, between-subjects design was deemed less favourable as the necessary 3.5-hour interval between administration and experimental testing would have introduced the opportunity for participants to practice the novel heartbeat tracking task. Nor, due to the Cyberball manipulation was it feasible to test each participant on two different occasions in a within-subjects design. However, given that randomisation of participant group allocation was ensured in a double-blind design, an acceptable degree of validity is ensured (De Ploy &

Gitlin, 2011). Nevertheless, future studies will instead benefit from testing baseline IAcc in a single, separate study, or by using alternative interoceptive measures such as gastric, respiratory or touch acuity (Garfinkel et al., 2017).

Secondly, it is customary to assess circulating levels of testosterone, either in saliva or blood, to confirm significantly elevated levels of testosterone in the treated group. Due to limited resources, we were not able to assess basal testosterone. However, based on previous studies that demonstrated a ten-fold increase in women's total testosterone in response to 0.5mg of the hormone (Tuiten et al., 2000), we can infer with a reasonable degree of confidence that the significant differences in IAcc between the hormone and placebo treated group during the heartbeat tracking task reflected activity of testosterone.

2.4.4. Conclusion

Our findings contribute to an emerging literature on the embodied basis of social power (Haas et al., 2016; Obhi, Swiderski & Brubacher, 2012; Moeini-Jazani et al., 2017; Werner et al., 2009). We show that 0.5mg of testosterone significantly increases interoceptive accuracy relative to placebo. From the perspective of embodied cognition, this gain in bodily feedback likely confers several advantages relating to the experience of control via the ability to successfully anticipate threat and experience bodily competence. In similar ways to physiological loss, social loss may be communicated by changes in the interoceptive system, highlighting the importance of iterative cycling between different modes of inference (Farb et al., 2015). Our finding in the testosterone group of a relative drop in IAcc following ostracism could be interpreted as a novel mechanism via which social vigilance is regulated. Changes in bodily awareness may function to signal not only physiological loss but also social loss. Feeling out of control may provide the motivational impetus toward reinstating it. Finally, the modulation of interoceptive processing by testosterone indicates that levels of IAcc are state-like with adaptive functions that appear to be context-specific. However, our effect sizes were modest, derived from a sample of women only and should be interpreted cautiously. Future studies on this topic will benefit from larger sample sizes and the inclusion of men to further investigate the social implications of the effect of hormones on interoceptive processing.

Chapter 3 | Experiment two: The territory of my body: Testosterone prevents limb cooling in the Rubber Hand Illusion

3.1 Introduction

Several decades of research point to the steroid hormone, testosterone, as a key determinant of socially dominant behaviours that promote self-interests and the acquisition of power and high status in group hierarchies (Carré & Putman, 2010; van der Westhuizen & Solms, 2015a; Ronay & von Hippel, 2010). For example, testosterone facilitates resilience in stressful situations (Enter, Spinhoven & Roelofs, 2014; Hermans et al., 2007; Russo et al., 2012) and increases the motivation to approach social challenge as a means of achieving dominance in potentially hazardous social contexts (Terburg & van Honk, 2013). Some studies indicate that testosterone also regulates certain pro-social forms of behaviour too, but the defensive monitoring of implicit social threat (Hermans, Ramsey & van Honk, 2008; Terburg et al., 2012; van Honk et al., 1999) and the attenuation of certain empathic processes that might otherwise interfere with competition (Hermans et al., 2006) have been established as key mechanisms via which it regulates power and social status.

Currently, though the neural chemistries and patterns of behavioural gestures that support the acquisition of social power are well described in both humans and other species (for a review, see van der Westhuizen & Solms, 2015a), research is only now beginning to elucidate the sensory-motor profiles of the body that are modulated by social status. For instance, Moeini-Jazani et al., (2017) recently showed that increases in social power lead to improved perception of visceral bodily signals, argued by the authors to reflect a shift toward an internal locus of control. Individuals who score higher on measures of interpersonal sensitivity have also been shown to be more susceptible to bodily illusions (Kállai, Hegedüs, Feldmann, Rózsa et al., 2015). Together, these findings hint at the possibility that the experience of power and control may manifest firstly in the bodily domain before extending upwards to influence higher aspects of cognition and feeling.

This idea falls within the increasingly influential embodied cognition framework (Barsalau, 2008; Wilson, 2002), in which the body is viewed as a constituting factor in mental experience. Representations of the body therefore have direct implications for higher-order

aspects of self-consciousness, and bodily signals of all kinds – whether affective, sensory or homeostatic – have been argued in this way to constrain one’s experience in the world, even when the signals are outside of awareness (Gallagher & Aguda, 2015). Stimulating the muscular system through bodily gestures, like making a tight fist, for instance, tends to make men feel more powerful (Schubert & Koole, 2009). This is thought to occur because the body and its inherent phenomenology is used as a reference point for perceiving the world and extracting meaning. Brain mechanisms that regulate body ownership should therefore have significant consequences for psychological experiences related to social power, especially during exchanges involving *other* bodies.

3.1.1 Body Ownership

Body ownership is the feeling that “I am the subject of this thing, my body” and is thought to arise via the synchronous registration and integration of bodily signals from exteroceptive, interoceptive and proprioceptive modalities (Damasio 2000; de Vignemont, 2011; Ehrsson, 2012; Ehrsson, Spence & Passingham, 2005; Lopez, Halje & Blanke, 2008; Metzinger, 2003; Tsakiris, 2008; 2010). It is captured by a subjective feeling of *mineness* but possession of the physical body takes place implicitly too, from early on in development (Rochat & Hespos, 1997). This continuity between the self and the body in relation to others and the environment serves as an important construct for thinking about the social self (Gallese, Keysers & Rizzolatti, 2004; Maister et al., 2013) but also establishes the first-person perspective and functions as a mechanism that allows the subject to organize information and interact efficiently, and with a sense of familiarity, in rapidly changing settings (Damasio, 2010; Neisser, 1988; Metzinger, 2003). As such, body ownership must play an important role in adaptive, “approach” human behaviour, especially so in that it provides a reference point from which to appraise and actively respond to different kinds of stimuli in the immediate environment, including those that might be socially threatening.

3.1.2 Malleable body schemas and the RHI

‘Threat’, in fact – to the integrity of the bodily self – has played a key role in the study of changes in body ownership, which has been extensively investigated in a range of procedures that experimentally induce the feeling of ownership over “not me” body parts and even whole bodies (Salomon et al., 2013; Tsakiris, 2016). Several experimental paradigms that

manipulate multi-sensory integration have revealed that bodily self-representations are not rigid but that individuals differ in the extent to which their existing schema is malleable due to its multi-sensory nature and can be *replaced* by “not me” bodies and body parts (Botvinick & Cohen 1998; Constantini & Haggard, 2007; Tsakiris & Haggard 2005; Tsakiris et al. 2007).

In an experimental procedure referred to as the rubber hand illusion (RHI; Botvinick & Cohen 1998; Tsakiris & Haggard 2005), synchronous stroking of one’s own unseen hand and a rubber hand that is anatomically aligned with the body, leads to a feeling of ownership over the prosthesis as well as changes in the existing bodily matrix. The extent of the illusion can be quantified in both explicit and implicit ways, by: the subjective, self-reported feeling of ownership (Botvinick & Cohen 1998; Longo et al., 2008), by a shift in subjective perception of the real limb’s location towards the rubber hand (proprioceptive drift; Botvinick & Cohen 1998) and implicitly, by an objective drop in temperature in the real hand (Hohwy & Paton, 2010; Kammers, Rose & Haggard, 2011; Moseley et al., 2008; Thakkar, Nichols, McIntosh & Park, 2011; Tsakiris, Tajadura-Jiménez & Constantini, 2011; Van Stralen et al., 2014).

Moseley et al (2008) have suggested that a drop in limb temperature during the RHI can be interpreted as a disruption in the physiological regulation of the real hand, suggesting that homeostatic processes are affected by subjective ownership over the rubber (versus the real) hand. This is thought to reflect, on an implicit level, a disturbance in conception of the bodily self. Indeed, reductions in temperature have also been observed in the full-body illusion (Salomon et al., 2013). Although not all studies report a disturbance in thermoregulation (de Haan et al., 2017), in support of Moseley’s et al. (2008) view, several studies have shown that motor and sensory nerve conductivity and responsivity declines in response to cooling (Abramson et al., 1966; Dioszeghy & Stalberg, 1992; Halar, DeLisa & Soine, 1983; Herrera et al., 2010). In fact, della Gatta et al., (2016) report significantly reduced motor evoked potentials in the real hand following induction of the illusion and Barnsley et al. (2011) have demonstrated that histamine reactivity in the real hand of participants’ increases in response to the illusion. This implies that not only is ownership over a foreign limb attained, but that the motor and interoceptive systems react by “disowning” the real hand, as if it had become a foreign body (Tsakiris, 2017).

It is not yet clear whether these changes in minimal bodily consciousness have any meaningful bearing on adaptive, goal-oriented behaviour. Evidence does, however, suggest that blurring of self-other boundaries appears to be a function of socio-emotional variables, with several studies showing that ‘concern for others’, or empathic motivation, positively predict degrees of malleability in the subjective domain (Asai et al., 2011; Cascio et al., 2012; Paton et al., 2012). For instance, Ide and Wada (2017) recently found that salivary oxytocin, which is well known for its role in social nurturance and empathy (Panksepp, 1998), positively relates to subjective ownership in the RHI. Testosterone may therefore disrupt bodily plasticity, given its interference with empathic processing (Hermans et al., 2006).

Some preliminary evidence suggests that individuals with malleable body representations might have difficulty prioritizing their own needs. A study by Paladino et al. (2013) on multisensory integration in the enfacement illusion, a facial analogue of the RHI, showed that following the induction of an illusory feeling of ownership over another person’s face, participants were more likely to conform and defer to the judgement of this embodied “other”. People who lack experiences of power in their daily living also demonstrate lower interoceptive accuracy (Moeini-Jazani et al., 2017) – a predictor of more malleable body schemas (Tajadura-Jiminez et al., 2011) which is also closely linked to psychiatric disturbance (Bender et al., 2007; de Bonis et al., 1995; Noel et al., 2017). This may occur because disembodiment reduces the flow of relevant bodily information that a subject uses to monitor how well they are faring in a current situation (Pezzulo, Rigoli & Friston, 2015).

In keeping with embodied cognition theories, disowning the body thus appears to relate in fundamental ways to emotional functioning and the fact that not all RHI studies (David et al., 2014; Dehaan et al. 2017; Grynberg & Pollatos, 2015; Paton et al., 2012; Rohde et al., 2013; Thakkar et al., 2011) report consistent drops in limb temperature further supports a role for specific emotional variables as contingencies in this regard. If such variables are not controlled for, they may cancel out at the group level any reliable change in homeostatic regulation. Thus, the link between social emotions and body ownership strongly suggests a role for testosterone in the modulation of corporeal experience.

3.1.4 Overview and aims

In sum, the RHI is well established as an experimental paradigm for undermining the integrity of the bodily self. Bodily self-consciousness has direct implications for mental experience because we draw on bodily states to evaluate and respond to “not me” objects in the external environment. The capacity for embodiment is therefore potentially empowering and disembodiment, by contrast, could be argued to reflect a state of disempowerment. Here we explore the idea that effective maintenance of the body’s representational boundaries can be regarded, conceptually, as a defensive state facilitating integrity of the self. Using a double-blind, placebo-controlled design, this study examined the effects of 0.5mg testosterone on three indices of the RHI in a sample of women, including subjective feelings of ownership, proprioceptive drift and objective changes in limb temperature.

3.2 Methods

Ethical approval was granted by the University of Cape Town’s Human Research Ethics committee (HREC REF 868/2014). All data was collected in accordance with the Declaration of Helsinki. Informed consent was obtained prior to commencement of the study and a debriefing took place upon completion of data collection. There were no reports of negative side effects from the testosterone or placebo administration and no participant withdrew from the study.

3. 2.1 Participants

48 neurologically healthy, right-handed female participants, aged between 18 and 30 years were recruited to participate in the study in exchange for 18 USD. Testing was performed during the pre-ovulatory phase of the menstrual cycle since androgen levels are relatively constant during this time. Participants were provided with a calendar at first contact to help them track their cycle and menstrual phase was confirmed again the day before testing. Individuals who were taking any form of hormonal contraception or other form of medication were excluded from participation, as were those with a history of psychiatric illness. We excluded males as the reliability of the testosterone administration protocol has only been firmly established in females (Tuiten et al., 2000).

3.2.2 Self-report measures

3.2.2.1 Profile of Mood States (POMS) abbreviated questionnaire

We employed the POMS (Shacham, 1983) to assess whether indices of the RHI in the placebo group were influenced by current mood state, since positive emotions may be a proxy for social coping and resilience. The POMS consists of 40 adjectives that measure depression, anger, confusion, vigour and fatigue. It was completed at the beginning of the experimental session. A Total Mood Disturbance (TMD) score was calculated by adding together the scores for Tension, Depression, Anger, Fatigue and Confusion and then subtracting the score for Vigour.

3.2.2.2 Self-report questionnaire for the RHI

Following Tsakiris, Tajadura Jiménez and Costantini (2011), who abridged and validated Longo's (2008) original 27-item self-report questionnaire for the RHI, we used their 8-item version. This self-report questionnaire for the RHI provides a measure of the subjective experience of the induction of the illusion and was based on a qualitative study where five participants were encouraged to freely report their experiences after induction. The abridged version focusses on themes relating specifically to body ownership (first 5 items) and location of the real hand in relation to the rubber hand (last 3 items), and makes use of a Likert scale where scores can range from 1 (strongly disagree) to 7 (strongly agree) with 4 being neither agree nor disagree, amounting to a total possible score of 56. Refer to Table 3.1 for a list of these 8 items.

3.2.3 Apparatus and procedures

Participants were randomly assigned to either the testosterone or placebo group and tested on one occasion in a double-blind, between-subjects design. To control for hormonal fluctuations in diurnal cycles, testing sessions were standardised to the afternoon. Participants reported to the lab exactly 4 hours prior to the experimental session at which time they received sublingual administration of testosterone or placebo. This schedule was based on previous research which has shown the efficacy of sublingual testosterone administration to peak after 4-6 hours (Hermans et al., 2006; 2007; 2008; Montoya et al., 2013; Terburg et al., 2012; Tuiten et al., 2000; van Honk, 2004; 2005). The testosterone

administration consisted of 0.5mg of testosterone, 5mg of the carrier hydroxypropyl beta cyclodextrin, 5mg ethanol and 5ml of water. For the placebo administration, the 0.5mg of testosterone was omitted. The administrations were identical in taste and delivered blind in coded vials. During the interval, participants were requested to refrain from engaging in strenuous or sexual activity, to avoid smoking or consuming excessive caffeine or consuming a heavy meal less than one hour prior to the experiment.

Table 3.1. Items from the RHI self-report questionnaire.

1	It seemed like I was looking at my own hand, rather than at a rubber hand.
2	It seemed like the rubber hand was a part of my body.
3	It seemed like the rubber hand was my hand.
4	It seemed like the rubber hand belonged to me.
5	It seemed like the rubber hand began to resemble my real hand.
6	It seemed like the rubber hand was in the location where my hand was.
7	It seemed like the touch I felt was caused by the paintbrush touching the rubber hand.
8	It seemed like my hand was in the location where the rubber hand was.

Items 1-5 gauge subjective ownership more explicitly and can be scored separately out of 35.

The RHI was carried out in accordance with standard procedure (Tsakiris & Haggard, 2005) and operationalised in terms of a self-report questionnaire, measures of proprioceptive drift and temperature change in the experimental limb. The researcher and participant sat opposite one another at a table, separated by a rectangular box with openings on either side so that the researcher could see the participant's left hand resting inside the structure (See Figure 1). The rim of the top surface of the box on the side facing the experimenter included a ruler to track hand position estimates. A life-like, plastic, left-hand prosthesis was custom made. Prior to the study, a temporary mould was constructed from alginate and filled with liquid, casting resin. During the experiment, the prosthesis was placed next to the box in the same orientation as the participant's real left hand at a distance of approximately 30cm away. Prior to placement, participants were presented with three prostheses, differing in terms of skin shade, and asked to select for use the one which they felt most closely resembled their own

skin colour. A dark smock was draped over the participant's shoulder to hide the position of their real left arm, leaving only the rubber hand visible.

The RHI task involved two blocks – an experimental-synchronous condition and a control-asynchronous condition – which were counterbalanced across participants. At the start of each block, the participant was instructed to place their left hand inside the box and look towards the prosthesis. Prior to induction, the RHI questionnaire was administered and a proprioceptive judgment was obtained by asking participants to use their free, right hand to indicate along the top surface of the box where they felt the nail of their left index finger was currently located. This location was quantified in terms of the corresponding location of the ruler, which was only visible to the researcher. A baseline temperature reading of the knuckle closest to the nail of the left hand index finger was then taken using an MT964 non-contact



Figure 3.1. The set up for the RHI requires that the participant is not able to see their real left hand while the prosthesis is in clear sight. For proprioceptive judgements, participants were questioned about the current location of their hand relative to position “1”. Temperature readings by infra-red thermometer were taken from location “2”. The box measured 40cm in width, 28cm in height and 23cm in depth.

infrared thermometer (Major-Tech Ltd.), which displays precision up to two decimal places. Following Tsakiris, Tajadura-Jiménez and Constantini (2011), only temperature on the experimental limb was recorded.

The first induction phase of the illusion was then performed for 120 seconds, during which the experimenter applied brush strokes at a speed of 1Hz using two identical paintbrushes to the participant's hidden hand and the prosthesis, to which, their gaze was fixed. Participants were instructed to remain still and refrain from talking during the induction. For the synchronous block, the brush strokes were administered at the same time, in synchrony, running from the knuckle of the index finger to the fingertip. In the asynchronous block,

brushstrokes to the prosthesis were applied 180 degrees out of phase (stroking began on the rubber hand between 0.5-1 second before tactile stimulation of the real hand).

Immediately following the stroking phase, a second temperature reading was taken and the participant was requested to make another proprioceptive judgment before removing their hand from the box and filling in the RHI questionnaire once more. Between blocks, participants were asked to briefly stand up so as to encourage the “re-setting” of sensory-motor parameters between stroking conditions.

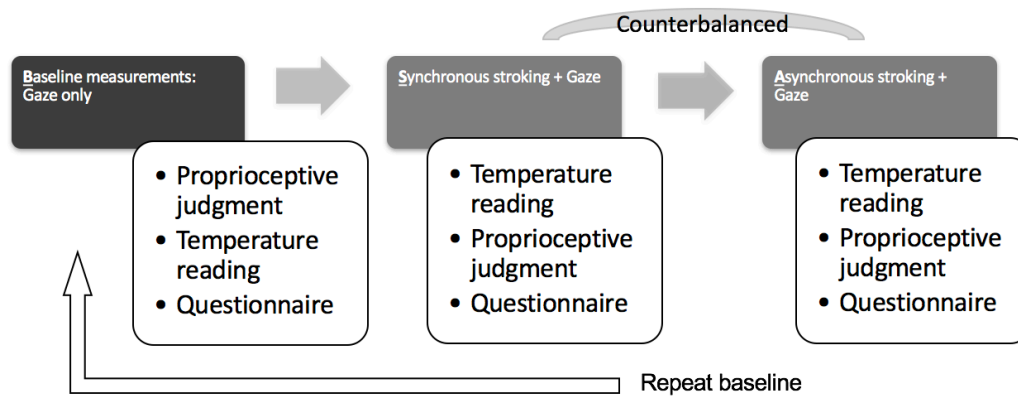


Figure 3.2. Schematic overview of the procedure and recording schedule for subjective ownership, proprioceptive and physiological temperature changes during the RHI induction. Baseline measures are recorded prior to induction in each stroking condition to control for changes attributed solely to the observation of the prosthesis (visual capture).

3.2.4 Analysis of the RHI

Table 3.2. Calculation of differential variables for analysis

Baseline Corrected (BCC) Scores of Change:

Synchronous (S) Condition

Post-stroking self-report – Baseline =	BCC Self-report (S)
Post-stroking proprioception – Baseline =	Proprioceptive drift¹ (S)
Post-stroking temperature – Baseline =	BCC Temperature³ (S)

Asynchronous (A) Condition

Post-stroking self-report – Baseline =	BCC Self-report (A)
Post-stroking proprioception – Baseline =	Proprioceptive drift (A)
Post-stroking temperature – Baseline =	BCC Temperature (A)

Perceptual/Physiological Shift (PS)

Scores:

Self-report PS =	BCC Self-report (S) - BCC Self-report (A)
Proprioceptive PS² =	Proprioceptive drift (S) – Proprioceptive drift (A)
Temperature Shift⁴ =	BCC Temperature (S) - BCC Temperature (A)

^{1,2} Negative values indicate a shift toward the rubber hand. ^{3,4} Negative values indicate greater reductions in temperature in response to stroking.

The RHI procedure results in several indices that allow one to control for both visual capture, i.e., the effect on illusory changes occurring as a result of simply processing the visual properties of the prosthesis without simultaneous tactile input, as well as the effect of multi-sensory integration induced specifically by synchronous stroking. The first baseline reading at the very start of the experiment was used to compare existing differences on each measure across placebo and testosterone groups.

Thus, to compute scores that control for visual capture and which represent the change as a result of stroking in both conditions, baseline measures prior to stroking of the subjective experience of the illusion, proprioceptive judgements and temperature readings were subtracted from post-induction scores in each stroking condition. For proprioception, this value is referred to in the literature as “proprioceptive drift”. These scores, which we will call ‘baseline corrected change’ (BCC), were then used to calculate the specific influence of multi-sensory integration, which is of key relevance to the manifestation of body ownership. These critical values are referred to as the Perceptual Shift and are calculated by subtracting scores from the Asynchronous condition from scores in the Synchronous condition. Refer to Table 3.2 for an overview of these differentials.

3.3 Results

Prior to analysis, the data was screened and outliers were removed if they exceeded 3 standard deviations plus/minus the mean. Review of the self-report data revealed 1 outlier in each group. A further outlier was found in the proprioception data. 1 participant failed to provide a full data set for the self-report questionnaire. Data sets from 2 further participants were excluded due to noncompliance with the experimental instructions (movement), leaving a total sample of 46 for temperature and proprioception indices and 44 in the self-report pool.

The testosterone and placebo groups did not differ significantly on any measure of the RHI at baseline (Self-report questionnaire: $t_{42} = .32, p = .75$; Proprioceptive mislocalisation: $t_{44} = 1.59, p = .87$; Limb temperature: $t_{44} = .81, p = .42$. Mean values are displayed in Table 3. This implies that the groups were comparable at the start of the experiment in terms of their hand temperature, their proprioceptive representations and their subjective perceptions of the prosthesis.

Table 3.3.

Baseline and baseline-corrected (BC) descriptive statistics for measures of the RHI

Mean (SD)

Baseline Values	Placebo	N	Testosterone	N
Self-report questionnaire ²	22.8 (9.72)	22	21.9 (9.03)	22
Proprioceptive mislocalisation (cm)	3.00 (2.85)	23	2.9 (2.62)	23
Temperature (°Celcius)	28.4 (3.78)	23	27.5 (3.72)	23
Asynchronous Condition				
Self-report questionnaire BC	8.14 (12.96)	22	6.59 (11.31)	22
Proprioceptive mislocalisation (cm)	.27 (1.97)	23	-.43 (2.39)	23
Temperature BC (°Celcius)	.01 (.70)	23	-.22 (.81)	23
Synchronous Condition				
Self-report questionnaire BC	18.32 (12.20)	22	20.41 (13.78)	22
Proprioceptive mislocalisation (cm)	-.52 (1.23)	23	-1.30 (1.47)	23
Temperature BC (°Celcius)	-.46 (.79)	23	-.01 (.71)	23

¹Baseline-corrected (BC) scores reflect the unique contribution of multi-sensory integration processes happening in the synchronous condition. ²Out of a total score of 56.

3.3.1 Self-report questionnaire

Mean scores on the self-report questionnaires were submitted to a mixed ANOVA, with stroking condition (visual-tactile stimulation) as the within-subjects factor and group (placebo versus testosterone) as the between-subjects factor. There was a significant main effect of visual-tactile stimulation ($F_{1,42} = 38.111, p < .00$). Across groups, scores for subjective experience of the illusion were higher following synchronous stroking, indicating that the procedure successfully induced the illusion. There was no main effect for group ($F_{1,42} = .01, p = .93$), nor was the interaction significant ($F_{1,42} = .86, p = .36$), suggesting that there was no specific effect of testosterone on either stroking condition. Looking at the self-report perceptual shift variables, an independent samples t-test showed no significant differences between the groups ($t_{42} = -.94, p = .36, d = .28$). These results indicate that testosterone had no effect on the subjective experience of the RHI.

We then looked to see if there was a difference between the two groups on the first five items of the self-report questionnaire, which focus more specifically on the subjective feeling of

ownership over the rubber hand (the latter three items inquire about the subjective experience of limb location). Groups did not differ at baseline ($t_{42} = .39, p = .69$). Refer to Table 1 to view these items. ANOVA results indicated that there was a main effect of visual-tactile stimulation ($F_{1,42} = 44.18, p < .00$). Both placebo ($M=14.18, SD=7.08$) and testosterone ($M=15.26, SD=8.30$) groups showed substantially increased ratings of subjective ownership for the synchronous stroking condition. There was however no significant interaction effect ($F_{1,42} = .70, p = .41$) implying that neither group was specifically influenced by a multi-sensory effect. A two-tail t-test comparing the perceptual shift of these 5 subjective ownership items confirmed this finding, revealing no significant difference between testosterone and placebo groups ($t_{42} = -.84, p = .41, d = .25$).

3.3.2. Proprioceptive drifts

Average proprioceptive drifts were analysed using a mixed ANOVA, with stroking condition (visual-tactile stimulation) as the within-subjects factor and group (placebo versus testosterone) as the between-subjects factor. There was a main effect for stroking condition ($F_{1,44} = 4.104, p = .04$) and for group ($F_{1,44} = 4.24, p = .04$). Participants tended to perceive their hand as being closer to the rubber hand following synchronous stroking compared to asynchronous stimulation. Furthermore, collapsing across conditions, the testosterone group displayed significantly more proprioceptive drift than the placebo group. However, there was no interaction effect ($F_{1,44} = .01, p = .94$) and, confirming this, an independent samples t-tests of the proprioceptive drift perceptual shift variables showed no significant difference between the two groups ($t_{44} = .08, p = .94, d = .02$).

3.3.3 Temperature change

Scores reflecting the change in limb temperature were submitted to a mixed ANOVA, with stroking condition (visual-tactile stimulation) as the within-subjects factor and group (placebo versus testosterone) as the between-subjects factor. There were no main effects for stroking ($F_{1,44} = 1.33, p = .25$) or group ($F_{1,44} = .32, p = .58$); however, the interaction was significant ($F_{1,44} = 9.020, p = .004$). Independent samples t-tests (one-tailed) were used to compare the change in temperature between the two groups for each stroking condition. Following synchronous tactile stimulation, the temperature change between the testosterone and placebo groups was significant ($t_{44} = -2.018, p = .02$). In contrast, temperature change

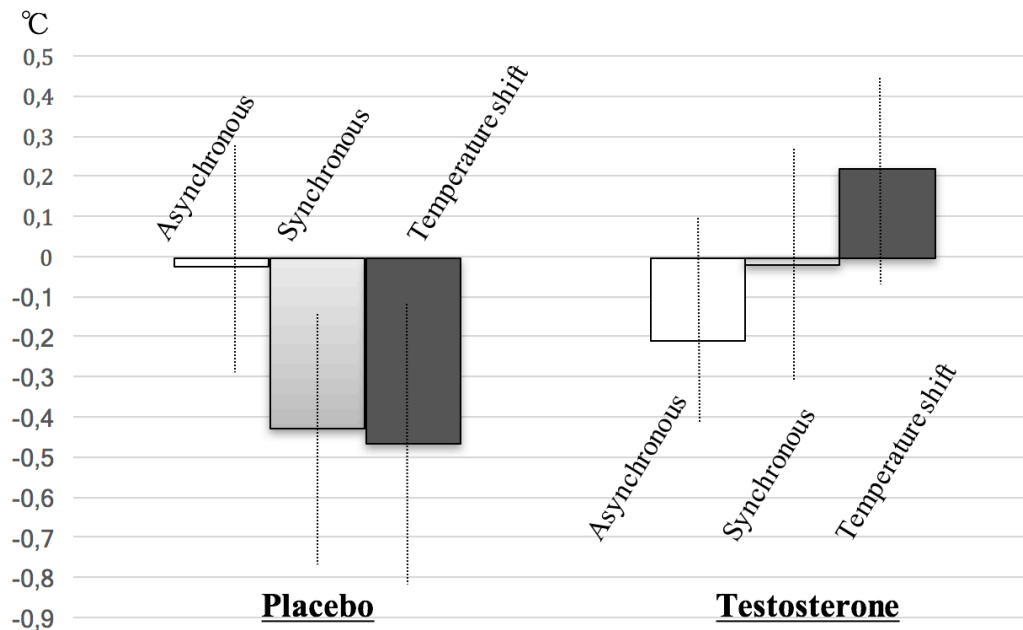
did not differ significantly between testosterone and placebo groups following the asynchronous condition ($t_{44} = 1.03, p = .31$). To further explore the interaction, paired sample t-tests (2-tailed) were used to test differences in temperature change scores within groups between stroking conditions. There was a significant difference between the synchronous and asynchronous stroking condition in the placebo group ($t_{22} = -2.69, p = .01$), but not in the testosterone group ($t_{22} = 1.45, p = .16$).

T-tests indicated that the drop in limb temperature from baseline to post-induction in the synchronous condition was significant in the placebo group only ($t_{22} = 2.737, p = .006$), who dropped by .457 degrees Celsius, but not in the testosterone group ($t_{22} = .06, p = .43$), where only a .009 decrease was observed. There were no significant differences between baseline and post-induction temperature scores in the asynchronous condition in the placebo ($t_{22} = -.09, p = .93$) nor the testosterone group ($t_{22} = 1.29, p = .21$).

Corroborating these findings, an independent samples, two-tailed t-test comparing the shift in temperature change from asynchronous stroking to synchronous stroking (temperature shift) showed a significant difference between testosterone and placebo groups ($t_{44} = -3.003, p = .004, d = .89$). These results indicate that limb temperature dropped significantly in response to synchronous tactile stimulation in the placebo group, but no such effect occurred after administration of testosterone.

Finally, as a control measure, since the testosterone group had marginally but not significantly higher temperature readings at baseline, we looked to see if temperature drops in the synchronous condition occurred simply as a function of higher pre-test limb temperature. A t-test indicated that there were no significant differences in temperature change between participants who had categorically low versus high baseline limb temperature ($t_{44} = -.244, p = .81$).

Figure 3.3. Effects of testosterone versus placebo on limb temperature change across conditions



During the Synchronous stroking condition, participants in the placebo group demonstrated a significant drop in limb temperature while no such drop occurred in the testosterone group. ‘Temperature shift’ is the difference between synchronous and asynchronous change and represents the unique contribution of multi-sensory processes. Error bars denote s.e.m.

Relationships between the perceptual shift indices of the RHI were assessed in the placebo group only. The self-report questionnaire was negatively correlated with temperature change ($r(23) = .44, p = .04$). However, after applying a Bonferonni correction for multiple comparisons, this finding was no longer significant. Looking specifically at the 5 items which focus on the subjective experience of ownership, there was a moderate to strong negative correlation with temperature drop, which remained significant after correcting for multiple comparisons ($r(22) = -.57, p = .006$). This finding implies that greater drops in limb temperature were associated with increased ratings of ownership over the rubber hand. Proprioceptive drift was not significantly related to subjective ownership ($r(22) = -.30, p = .17$) or temperature shift ($r(23) = -.06, p = .78$).

3.3.4 Mood data

There were no significant differences between the placebo and testosterone group on any sub-scale of the POMS, nor did the composite score, reflecting total mood disturbance (TMD), differ between the two groups ($t_{42} = .29, p = .77$). Correlation analyses of the mood data and indices of the RHI in the placebo group indicated that TMD was positively related

to proprioceptive shifts toward the rubber hand ($r(22) = -.59, p = .004$). This result survived a Bonferroni correction which specifies an alpha of .016 for significance. TMD was not related to temperature changes ($r(22) = .17, p = .44$) nor subjective reports of ownership over the rubber limb ($r(21) = .23, p = .32$).

3.4 Discussion

Working within an embodied cognition framework, in this study we explored the hypothesis that effective maintenance of the body's representational boundaries can be regarded, conceptually, as a defensive state facilitating the integrity of the self. We anticipated resistance toward the RHI in a sample of women administered 0.5mg of testosterone, a steroid hormone well known to promote defensiveness (Terburg et al., 2012; van der Westhuizen & Solms, 2015) and motivations for dominance and power (Carré & Putman, 2010; Eisenegger et al., 2011; van der Westhuizen & Solms, 2015a; Ronay & von Hippel, 2010). Testosterone had no effect on the subjective experience of the RHI or on measures of proprioceptive drift in comparison to placebo. However, the group of participants administered testosterone failed to show the same decline in limb temperature in response to synchronous tactile stimulation, as was seen in the placebo group. This effect does not likely reflect a uniform thermal advantage, since the groups did not differ in limb temperature at baseline. Furthermore, collapsing across the sample, temperature drops did not occur as a function of higher baseline temperature. Thus, while explicit bodily representations were unaffected by testosterone, our hypothesis was confirmed in relation to implicit bodily representation, in that physiological processes related to thermoregulation operating outside of conscious awareness were maintained after administration of testosterone, but not after placebo.

3.4.1 Dissociable mechanisms

Consistent with several recent studies (Hohwy & Paton, 2010; Kammers, Rose & Haggard, 2011; Moseley et al., 2008; Thakkar, Nichols, McIntosh & Park, 2011; Tsakiris, Tajadura-Jiménez & Constantini, 2011; Van Stralen et al., 2014), induction of the RHI in the synchronous stroking condition lead to a significant decrease in limb temperature in the placebo group. The drop in temperature was of similar magnitude to that reported by Van Stralen et al. (2014) who employed an identical method. In their seminal study, Moseley et

al. (2008) showed that cooling of the real hand is not a simple corollary effect of simultaneous visual-tactile input *per se*, nor due to a shift in attention away from the real hand, but that it is specifically the disruption in the subjective feeling of ownership that causes the drop in temperature. As such, they proposed that cooling should be interpreted as a disturbance in the physiological regulation of the real hand.

Not all studies report reliable or consistent changes in limb temperature (David et al., 2014; Dehaan et al. 2017; Grynberg & Pollatos, 2015; Paton et al., 2012; Rohde et al., 2013; Thakkar et al., 2011). Hohwy and Paton (2010) documented a drop in temperature from synchronous stroking, but not in all variants of the illusion that correspond with an equal strength in subjective ownership. Another study found a decrease in both the experimental and control conditions, leading these authors to argue that a thermal change is not a strict correlate of the experience of ownership (Rohde, Wold, Karnath & Ernst, 2013). Indeed, while the current findings show that reductions in temperature and feelings of ownership are significantly correlated under placebo, the finding that the cooling effect was not seen in the testosterone group supports the view that temperature changes and explicit feelings of ownership reflect dissociable but related mechanisms. Whether the two coincide may be determined by other factors, such as circulating hormones.

It could be argued that implicit processes which directly correlate with bodily homeostasis have more immediate significance for the *re-acting* individual (eg. During social competition), unlike explicit awareness which arguably emerged later in phylogenetic development (Panksepp, 1998) and which is relatively superfluous to rapid motor-control (Cole & Paillard, 1995). This distinction may underlie a dissociation between homeostatic and subjective aspects of body ownership. Autonomic investment might be seen here as an indicator of active, first-person embodiment, that is, “I” (subject) versus “me” (object) (Babo-Rebelo, Richter & Tallon-Baudry, 2016). In support of this idea, Tsakiris Tajadura-Jiménez, and Costantini (2011) recently demonstrated that individuals with lower interoceptive awareness, a sensory channel argued to be critical in the foundation of stable bodily consciousness (Damasio, 2011), tend to react with larger drops in limb temperature in the RHI. This same group of individuals are known to experience body incompetence and the tendency to objectify the self (Ainley & Tsakiris, 2013). Our findings therefore suggest a role for testosterone in the maintenance of robust, *implicit* bodily representations that may

support action. Explicit, body-as-object representations appear, on the other hand, to be less influenced by testosterone.

3.4.2 Testosterone and self-other boundaries

Several studies have interpreted findings from the RHI in terms of self-other discrimination, that is, the ability to distinguish “me” and “not-me” percepts, actions and feelings. Self-other blurring, especially at the level of external body representations, has been linked to conformity behaviour (Paladino et al., 2010) and the activity of oxytocin (Ide & Wada, 2017). It is possible therefore that maintenance of limb temperature in response to the RHI may function as a protective mechanism against self-other blurring. In support of this, in our placebo sample, we observed a significant negative association between subjective ownership and limb cooling, suggesting that subjective identification with a “not me” body part was associated with disinvestment of the bodily self.

However, the pattern of findings in the hormone-treated group does not suggest that testosterone promotes, necessarily, a *distinction* between self and other during induction of the illusion, since we report comparable scores of subjective feelings of ownership. Nor, unlike those observed in the placebo group, do the findings indicate self-other blurring, ie., when subjective identification with the rubber hand corresponds with homeostatic disembodiment of the real hand. Instead, our results in the testosterone group show a *self-self* pattern. Participants in this group demonstrated the same capacity to embody the rubber hand while maintaining physiological regulation of their own hand. It is as if this group “gained” a limb while for the placebo group, the real hand was replaced by the prosthesis.

Disproportionate representation of ‘self’ likely predisposes to egocentric ways of thinking. Previous work supports this view in that testosterone not only has detrimental effects on aspects of social cognition, such as automatic facial mimicry (Hermans et al., 2008) but also on the ability to collaborate effectively with others in group settings (Wright et al., 2012). More interestingly, Overbeck and Droutman (2013) have argued that the use of the self as a heuristic for inferring the internal states of others is regularly seen in socially powerful people because of the strong link between the powerful and their roles in the leadership domain as the ones who are to represent the group at large. Being in power, or feeling powerful, may therefore prompt individuals to rely more on their own thoughts and

sensations. This relationship may function in both directions. Thus, having a self-anchored frame of reference, which in the context of the RHI may reflect in the preservation of implicit body boundaries, appears to be closely linked to testosterone dynamics and positions of status in group hierarchies.

Despite findings being consistent with a self-self pattern in the hormone-treated group, it is nonetheless surprising that subjective ownership in the RHI was not decreased by testosterone since empathy has been established as a predictor of subjective ownership but tends to be hampered by the administration of testosterone (Hermans et al., 2008; Montoya et al., 2013). This calls into question a simple, straightforward link between self-reported feelings of ownership and empathy, suggesting that the role of self-other blurring in empathic processing is more nuanced. For example, Colonnello et al., 2013 found that oxytocin administration facilitated participants ability to recognize themselves in self-other morphed images. Empathy is a complex emotional reaction, not likely to simply emerge from perceptual-motor simulations but may require ‘something more’ at the motivational level. This *something more* may depend on development and perhaps it is only individuals who are able to maintain *some* level of self-differentiation that exhibit higher levels of social altruism when subjective identification with another body is strong. Indeed, the ability to differentiate between self and other is key for successfully empathising with other minds because a loss of self may lead to excessive negative affect and subsequently impoverished helping efforts (Decety & Sommerville, 2003).

3.4.3 Testosterone and the preservation of the bodily self

From a Bayesian brain perspective (Pezzulo, Rigoli & Friston, 2015), top-down models that guide action must be anchored to the bodily, interoceptive self if they are to succeed in serving power and self-interests. Without doing so, predictive models of the self would be ineffective. Maintaining thermal homeostasis in the context of the RHI may help therefore to ensure stability and unity of the agentive, bodily self via enabling access to “gut feelings” (Dunn et al., 2010). The putative role for testosterone in the preservation of the bodily self is consistent with numerous studies associating the hormone to defensive, self-serving behaviour in humans and animals (Eisenegger et al., 2011; Dreher et al., 2016; Terburg et al., 2012; Wright et al., 2012). Via its influence on the amygdala and insular cortex, for instance, testosterone sustains threat monitoring (Bos et al., 2010; Hermans, Ramsey & van

Honk, 2008). Since the insula has also been linked to sensory-motor agency (Farrer & Frish, 2002) and body ownership (Karnath & Baier, 2010), the effect of testosterone on homeostatic resistance to RHI manipulations may be mediated, in part, by insula activity. This link reinforces the proposal that defence of body boundaries might be recruited in the service of more complex forms of motivated, defensive behaviour.

Of the studies performed on the RHI to date, none have directly explored the emotional correlates of temperature changes. It is therefore difficult to align the current findings of testosterone with prior research in the field. However, in other contexts, there appears to be a reliable link between reductions in skin temperature of the limbs and negative, largely disempowering emotional states. Several studies report drops in surface skin temperature in response to cognitive or emotional stress (Boudewyns, 1976; Bugental & Cortex, 1998; Mittleman & Wolff, 1939; Or & Duffy, 2007; Zhai & Barreto, 2006) and music that elicits negative emotional feelings (McFarland, 1985). Rimm-Kaufman and Kagan (1996) report a decrease in limb temperature in response to threatening personal questions but not to cognitive tasks or fear-eliciting film clips. Corroborating this, social ostracism has also been found to lower skin temperatures (Ijzerman et al., 2012), suggesting perhaps that a cooling of the body contributes to the implicit understanding of what it means, biologically and psychologically, to be socially threatened and disempowered. This link may apply exclusively to effector limbs, since increases in cheek temperature, as in the case of blushing, tends to be associated with social anxiety (Voncken, & Bögels, 2009; see also Nakanishi & Imai-Matsumura, 2008). Indeed, within the body, a drop in skin temperature appears to be related to reduced blood flow as a result of vasoconstriction which occurs following activation of the sympathetic nervous system (Wallin, 1981), i.e, the central stress response. It is possible, that on an implicit level, the RHI manipulation is experienced as a stressor, given that it threatens bodily integrity, and in this way may activate the stress response. Most notably, testosterone administration has been shown to attenuate responsiveness of the integrated stress system (Hermans et al., 2007), possibly explaining its ability to maintain skin temperature. Plausibly, such thermoregulatory effects would impact upon the sensation of effort, which is a key phenomenological aspect of motor control (Pacherie, 2008). Together, these findings imply that maintenance of body temperature is psychologically stabilising. The advantages to social coping achieved by those with higher levels of testosterone (Edwards, Wetzel & Wyner, 2006; Enter, Spinhoven & Roelofs, 2014; Rowe et al., 2004; van Honk et al., 2004) may thus derive from similar embodied mechanisms.

Finally, the effect of testosterone on preserving bodily representations during the illusion is also consistent with the finding that larger errors in proprioception, as a result of multisensory integration, were related to significantly higher levels of mood disturbance in the placebo group. Even though we did not observe any influence of testosterone on mood or proprioception directly, these findings nonetheless indicate that emotional factors do impinge on bodily representations. Specifically, here we show that negative mental states appear to “loosen” the bodily schema. Similarly, Kállai et al. (2015) report an association between *harm avoidance* and proprioceptive drift. That we did not observe any relationship between temperature shift and mood, or between testosterone and proprioceptive mislocation, suggests that thermoregulatory changes in the context of the RHI may reflect unconscious or implicit mental states. For instance, testosterone in particular is known to produce many of its emotion-regulating functions outside of conscious awareness (van Honk, Peper & Schutter, 2005). This might explain why it has no specific effect on proprioception during multi-sensory integration. It is, however, possible that the relationship reported here between mood items of the POMS and proprioceptive drift simply reflect reduced attention as a result of the negative mood states. As such, future studies will benefit from incorporating affective variables in RHI studies to advance our understanding of the emotional mechanisms influencing embodiment.

3.4.4 Limitations

The current findings should be considered with the following limitations in mind. A within-subjects would have afforded greater power and allowed us to assess whether the effect of testosterone on temperature in the RHI is a consistent phenomenon. Though the current findings cannot determine conclusively whether the maintenance of limb temperature derives from peripheral/bodily or central/brain mechanisms, it is worth noting that testosterone plays a key role in influencing the body by increasing muscular and skeletal strength (Bhasin et al., 1996) and by increasing the excitability of motor neurons (Maeda & Pascual-Leone, 2003; Ziemann, 2004). These metabolic and neural processes could be argued to influence thermoregulation in general. However, here we only observed a specific effect of testosterone on temperature in response to synchronous stroking. No such effect emerged in the control condition, implying that the effect of testosterone on thermoregulation is probably explained instead by a change higher up in the nervous system.

In support of this view, testosterone has been found to restore innervation of the peptide, arginine vasopressin, in the nucleus of the solitary tract (NST; Goudsmit, Fliers & Swaab, 1988), a key structure of the brain's interoceptive system receiving afferent input from the body periphery (Craig, 2003). The NST shows considerable androgenic immunoreactivity (Hamson, Jones & Watson, 2004) and furthermore, the brain's core temperature regulator – the medial pre-optic nucleus of the hypothalamus – receives projections directly from the NST (Ricardo & Koh, 1978). It is therefore possible that the preservation of thermoregulation by testosterone in the experimental limb might derive from activity in the brain.

3.4.5 Concluding remarks

In our sample, participants administered 0.5mg of testosterone failed to demonstrate the cooling of their own hand in response to the RHI, as was documented in the placebo group and several other recent studies (Hohwy & Paton, 2010; Kammers, Rose & Haggard, 2011; Moseley et al., 2008; Thakkar, Nichols, McIntosh & Park, 2011; Tsakiris, Tajadura-Jiménez & Constantini, 2011; Van Stralen et al., 2014). Previous authors have proposed that cooling should be understood as a disturbance in physiological homeostasis (Moseley et al., 2008). Drawing on embodied cognition theory, we propose that thermal regulation contributes to the effective maintenance of the body's representational boundaries and can be likened to a defensive state facilitating the unity of the self. Certainly, if not in reference to the self (i.e. without homeostatic investment in one's own body), the empowering nature of embodiment simply cannot occur. Indeed, one's own body is a space-occupying entity with an "inside" and an "outside" and, like any other territory, if the integrity of these boundaries are efficiently monitored, it provides stability. More significantly, a strongly defined self provides a means via which to expropriate valuable objects from the outside world via a process of self-association (De Dreu & Knippenberg, 2005; Turk et al., 2011). Based on our finding that testosterone prevents thermal deregulation during the RHI, we therefore speculate that the mechanism regulating homeostatic control over the body during multi-sensory integration in the RHI is an emotional one linked to self-preservation.

Chapter 4 | Experiment Three: Testosterone increases the sense of agency

4.1 Introduction

In neurologically healthy adults, voluntary actions tend to be accompanied by the distinct feeling of being able to control how one's actions and behaviours influence other people or the environment. This feeling is referred to as the sense of agency (SoA) and is the implicit sensation that arises when effected changes are attributed to one's own actions and not to other environmental factors or persons (Haggard & Tsakiris, 2009). For example, as I type the letter keys on my keyboard and focus my gaze on the screen, I have the strong feeling that I am causing the appearance of the text.

Once an obscure phenomenon considered a topic of philosophers only, neuroscientific research into the SoA has received a great deal of attention over the past several years. The brain mechanisms underpinning the SoA are multifaceted, involving both low-level sensory-motor and top-down inferential processes and are recruited differently depending on the context and availability of information in causal chains of events (Blakemore et al., 1998; Farrer et al., 2002; Haggard & Clark, 2003; Moore & Haggard, 2008; Sato & Yasuda, 2005; Wegner, 2002).

Though the feeling of agency is mostly taken for granted in one's everyday activities, aberrations in agency are seen in many self-limiting psychiatric disorders (Gentsch et al., 2012; Haggard et al., 2003; Obhi, Swiderski & Farquhar, 2013; Voss et al., 2010). Indeed, a robust and finely tuned sense of agency may have a number of advantages over an entirely cognitive means via which to establish cause and effect relationships (Caspar et al., 2016; Eitam, Kennedy & Higgins, 2013; David, Obhi & Moore, 2015; Pacherie, 2008). The implicit feeling that intentions are realized in the external world through voluntary actions and therefore under personal control is essential for the learning of action-effect relationships and thus for sustaining goal-directed behavior (Gentsch et al., 2015). This may be especially important in the social world where responsibility is often ambiguous and action outcomes are not always immediately apparent (de Bézenac et al., 2015; Pacherie, 2013).

Because the feeling of personal control over events in the environment is thought to be foundational for sustaining motivated behaviour and even the basic sense of free will (Gentsch et al., 2015; Moore, 2016), the SoA is closely linked to the experience of power

(Fast, Gruenfeld, Sivanathan, & Galinsky, 2009; Inesi et al., 2011). Many authors agree that the influence that power has on behaviour and perception (for example, selective attention, processing flexibility and optimism; Guinote, 2007; 2010; Anderson & Galinsky, 2006) can be explained in large part by the effects power has on an individual's basic sense of control (Galinsky, Gruenfeld & Magee, 2003; Guinote, 2010; Keltner, Gruenfeld & Anderson, 2003). In fact, Obhi, Swiderski and Brubacher (2012) have shown that although power priming did not increase agency, individuals made to feel powerless experienced less agency over their actions. Other authors have shown that implicit feelings of agency are rewarding and may thus provide a motivational impetus to act in much the same way as more tangible rewards (Karsh & Eitam, 2015). Such findings align closely with theories of embodied cognition, which assert that many complex mental states are grounded in more basic sensory-motor processes (Barsalou, 2008; Lackoff, 2012; Wilson, 2002). In other words, psychological meaning may derive from re-enactment of motor and perceptual states of the body. Perhaps, then, feeling powerful derives some of its phenomenology from more basic sensory-motor mechanisms of control. In this regard, the steroid hormone, testosterone, may be a potential modulator of the SoA because of its established role in the psychology of power (Ronay & von Hippel, 2009).

4.1.1 Testosterone and control

Throughout mammalian species of both sexes, testosterone has been linked to control over the social environment, pro-active or “approach” social motivation and power in group hierarchies (see Eisenegger, Haushofer & Fehr, 2011; van der Westhuizen & Solms, 2015). In affective neuroscience, the term “social approach” refers to the active pursuit of something desirable, particularly in threatening social contexts where the tendency to avoid is resisted (Terburg & van Honk, 2013). Testosterone tends to surge in social situations when one's status is threatened and its role in social approach motivation is evidenced by its link to social threat monitoring (Hermans, Ramsey & van Honk, 2008; Goetz et al., 2014; van Honk et al., 2001; van Honk et al., 1999), preference for high status (Josephs, Sellers, Newman & Mehta, 2006; van der Westhuizen & Solms, 2015b) and confidence (Baucom, Besch & Callahan, 1985), outgoingness (Dabbs & Ruback, 1988), assertiveness (Cashdan, 1995) or aggression (Cashdan, 2003).

From an embodied cognition perspective, this kind of social agency may depend in part on the same brain mechanisms that support sensory-motor agency. In corroboration, Pfister et

al., (2014) have shown that the SoA can emerge from actions that have social consequences. Thus, in social contexts, increased sense of agency over the behaviour of another agent may give rise to feelings of authority. Given that testosterone is known to promote affective states related to social empowerment, this suggests that fluctuations in testosterone may in turn modulate sensory-motor agency.

Several lines of evidence point to a potential role of testosterone in SoA. Firstly, in both male and female adults, grey matter volume in the insula, a brain structure which has been identified as a major substrate of the SoA (Farrer & Frith, 2002; Karnath & Baier, 2010), positively correlates with testosterone levels (Bos et al., 2011; Lentini et al., 2013). Secondly, the neurotransmitter dopamine not only maintains a great proportion of motivated behavior but has been linked to social dominance in several behavioral paradigms (Morgan et al., 2002; Winberg & Nilsson, 1992) and of significance, has also been shown to facilitate implicit feelings of volitional sensory-motor control (Moore et al., 2010). Testosterone is typically expressed in contexts where there is an opportunity to improve social status (Archer, 2006) and several studies have shown that it regulates the expression of dopamine in the brain (de Souza et al, 2009; Schroeder & Packard, 2000). Therefore, in such contexts, testosterone-mediated increases in dopamine may serve an adaptive role in social competition by facilitating feelings of personal control to encourage approach-related behaviour.

Finally, there is in fact some evidence, albeit indirect, to suggest that testosterone may encourage approach-related behaviour by acting on signals that prospectively contribute toward agency at the time of action selection, i.e., before the actual effects emerge, which is a potentially *illusory* manifestation of agency (Chambon & Haggard, 2012). Prospective mechanisms may be related in some instances to incentive processing, based on findings that reward priming increases the sense of agency (Aarts et al., 2012). Of relevance here, is that testosterone is known to facilitate incentive processing (Hermans et al., 2010), decrease fearfulness (Hermans et al., 2006; van Honk, Peper & Schuuter, 2005) and increase the excitability of motor neurons (Bonifazi et al., 2004). From an embodied cognition perspective, the basic experience of agentive control may not only contribute to the feelings of infallibility often associated with testosterone, but they may also constitute an important self-fulfilling mechanism by which power and dominance is initially achieved.

4.1.2 Overview of aims

In this study we used the perceived attraction in time between a voluntary action and its outcome as an implicit marker of SoA (Haggard, Clark & Kalogeras, 2002). When a person intentionally causes an event through one's own actions, the action and its consequence are experienced as being closer together in time. On the other hand, when we unintentionally cause an event (for example, if someone else causes us to move) we experience this unintentional movement and its consequence as further apart in time. This effect is known as 'intentional binding'. It is a widely used measure of SoA (see also Moore & Obhi, 2012, for a review).

In a placebo-controlled double-blind, repeated-measures study using 26 young women, we investigated if 0.5mgs of testosterone modulated intentional binding. We hypothesized that testosterone would increase intentional binding, in line with the idea that feelings of social control are founded upon more rudimentary experiences of sensory-motor control. While in real-world settings, testosterone tends only to surge in social contexts where status is at stake, in this experiment we artificially elevated testosterone levels to mimic the expression of testosterone in social settings. Thus, although our experiment was not social in nature, the administration of testosterone in one condition functioned to simulate a physiological reaction that would normally occur in a socially competitive situation (Bateup, Booth, Shirtcliff & Granger, 2002; Carré & Olmstead, 2015).

In a subset of the participant sample, we also investigated whether testosterone affected affective forecasting (Baron, 1992, Loewenstein & Schkade, 1999; Wilson & Gilbert, 1992), given that more optimistic perceptions of one's emotional state in the future has been linked to illusions of control (Taylor & Brown, 1998). Since the future is largely beyond one's control, and predictions are based on reconstructed memories (Schacter et al., 2012), optimistic perceptions about the future can be measured by comparing current and future mood states (Wilson & Gilbert, 2003). As two possible mechanisms that facilitate approach-oriented behavior, we therefore hypothesized that testosterone would increase SoA and promote positive expectations about the future.

4.2 Methods

Ethical approval was granted by the University of Cape Town's Human Research Ethics committee (HREC REF 868/2014). All data was collected in accordance with the Declaration of Helsinki. Informed consent was obtained prior to commencement of the study and debriefing took place upon completion of data collection. There were no reports of negative side effects from the testosterone or placebo administration and no participant withdrew from the study.

4.2.1 Participants

26 females, ranging between the ages of 18 and 30 from diverse ethnic backgrounds, were recruited to participate in the study in exchange for \$35. Males were excluded because the time course of effects for the current testosterone administration protocol have been reliably established in women only (Tuiten et al., 2000). Testing was performed during the pre-ovulatory phase of the menstrual cycle since androgen levels are relatively constant during this time. Participants were given a calendar and asked to track their menstrual cycle and were only allowed to be tested during the first ten days following the end of menstruation. Regrettably, we were not able to get serum or saliva samples to confirm basal testosterone levels. However, studies have shown that, controlling for factors like sexual activity, exercise and interpersonal conflict, testosterone levels are found to be highly reliable over a two week period (Liening et al., 2010). Finally, individuals taking any form of hormonal contraception or other form of medication were excluded from participation, as were those with a history of psychiatric illness.

4.2.2 Materials and Procedure

Participants were tested on two occasions within a one-week period¹ in a repeated measures, double-blind, placebo-controlled design. Drug condition order was counter-balanced across participants, who were randomly assigned to the testing schedule and assigned a participant code. To control for hormonal fluctuations in diurnal cycles, testing sessions were

¹ Specific testing days within the one week period were allocated on a convenience basis for each participant, but never on consecutive days.

standardised to 2pm. Each testing day required participants to report to the lab exactly 4 hours prior to the experimental session at which time they received sublingual administration of testosterone or placebo. This schedule was based on previous research which has shown the efficacy of sublingual testosterone administration to peak 4-6 hours later (Tuiten et al., 2000). The testosterone sample was comprised of 0.5mg of testosterone, 5mg of the carrier hydroxypropyl beta cyclodextrin, 5mg ethanol and 5ml of water. For the placebo samples, only the testosterone was omitted. Participants were made aware of that both testosterone and placebo formulas were identical to the taste. During the interval, participants were requested to refrain from engaging in strenuous or sexual activity, to avoid smoking or consuming caffeine. Before leaving, a scan of the participant's right hand was taken to measure the second-to-fourth digit ratio. Low ratios are thought to reflect greater prenatal exposure to testosterone in relation to estradiol (Lutchmaya et al., 2004) and have been found in other studies to moderate the effects of testosterone (Montoya et al., 2011; van Honk et al., 2011).

At the start of the experimental session, participants completed two versions of the Positive and Negative Affect Schedule (PANAS) (Watson et al., 1988). The scale consists of 2 subscales, each with 10 positive and 10 negative words, respectively that describe different emotions and feelings, for instance, "Excited," "Nervous," "Proud". Scores are summed for each subscale and then divided by 10 to get a mean value to represent each subscale. To assess current mood state, participants were asked to read each word and rate on a scale of 1-5 the extent to which they currently felt that way. In a second version, participants were asked to think about their future in a general sense and rate the degree to which they believed the word described their anticipated future mood state. The PANAS has been used previously in such a manner to determine affective forecasting (Wilson & Gilbert, 2003).

SoA was operationally defined in terms of "intentional binding", defined above and illustrated in Figure 1. The software for this task was developed in collaboration with our colleagues from UCT's computer science department and underwent thorough pilot testing to ensure its validity. In this classic task (see Moore & Obhi, 2012 for a review), participants are required, at a time of their choosing, to make voluntary button presses that trigger a tone. They are asked to watch a clock face at the centre of a computer screen, measuring 2.8cm in diameter and marked with conventional 5 "minute" intervals. A clock hand of 11mm rotated constantly at a speed of 2560ms per revolution.

Participants received both written and verbal instructions and had the opportunity to perform 5 practice trials. In agency conditions (operant blocks), participants made voluntary key presses that caused a tone after a 250ms delay. Participants judged the time of their key press or the subsequent tone, reporting the position of the clock hand when these events happened by typing the time into a response box at the end of each trial when the clock hand stopped rotating after a random interval between 1500 and 2500ms. Judgements were blocked (30 trials each), so participants only made a single type of estimate on each trial in each block. For each condition, the task always began with an operant block, followed by 30 trials of a baseline condition. Action and Tone condition order was counter-balanced between participants. In the baseline action block participants made voluntary key presses that did not produce a tone, and participants reported the time of the key press. In the baseline tone block participants made no key presses. Instead, a tone would sound at a random time on each trial and participants reported the time of the tone.

Action binding is found by subtracting the mean time estimate in the baseline action condition from the mean time estimate of actions in the operant condition. Action binding is indicated by a positive difference. Tone binding is found by subtracting the mean time estimate in the baseline tone condition from the mean time estimate of tones in the operant condition. Tone binding is indicated by a negative difference.

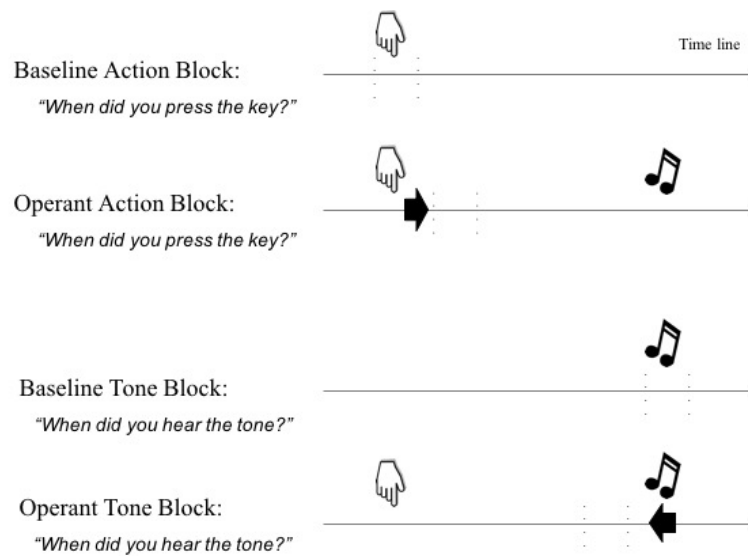
4.3 Results

Prior to analysis, outlying trials (>3 SD) in the intentional binding task were removed from each participant's individual data sets under the assumption that unusually large discrepancies between computer-recorded onset times and estimations made by participants reflect lapses in concentration. 16 outliers were removed and no participant recorded more than 2 such errors in a data set. Additionally, in both the Tone and Action Binding mean data sets, there was one outlying participant, leaving a final sample size of 25 for each condition.

4.3.1 Intentional binding

Descriptive statistics for separate baseline and operant blocks, and action binding and tone binding across testosterone and placebo conditions are displayed in Table 1. Global binding was calculated by subtracting tone binding from action binding.

Figure 4.1. The intentional binding task where perceptual shifts reflect binding.



In the Operant Action block, a tone follows the key press. When asked “When did you press the key?”, intentional binding is reflected by a shift in temporal awareness (dotted lines) toward the tone so that the participant reports a time that is later in time than the press actually occurred. For example, if the key press occurred at 15ms, the participant may report 25ms. In the Operant Tone condition, a tone always follows a voluntary key press. When asked, “When did you hear the tone?” there is an anticipatory effect and the participant tends to report the onset time of the tone as being earlier. For example, if the tone occurred at 45ms, the participant may report “30ms”. In baseline conditions, time reporting is not influenced by the action-effect relationship and tends to be more accurate.

Table 4.1 Mean shifts in time perception across testosterone and placebo treatment conditions

	Placebo		Testosterone	
	M	SD	M	SD
Action baseline	6.32	(72.38)	5.36	(50.13)
Action operant	22.12	(72.32)	43.8	(67.43)
Tone baseline	9.2	(58.36)	-9	(58.31)
Tone operant	-90.16	(114.7)	-102	(112.9)
Action Binding	15	(31.68)	38	(47.22)
Tone Binding	-99	(98.68)	-93	(101.92)

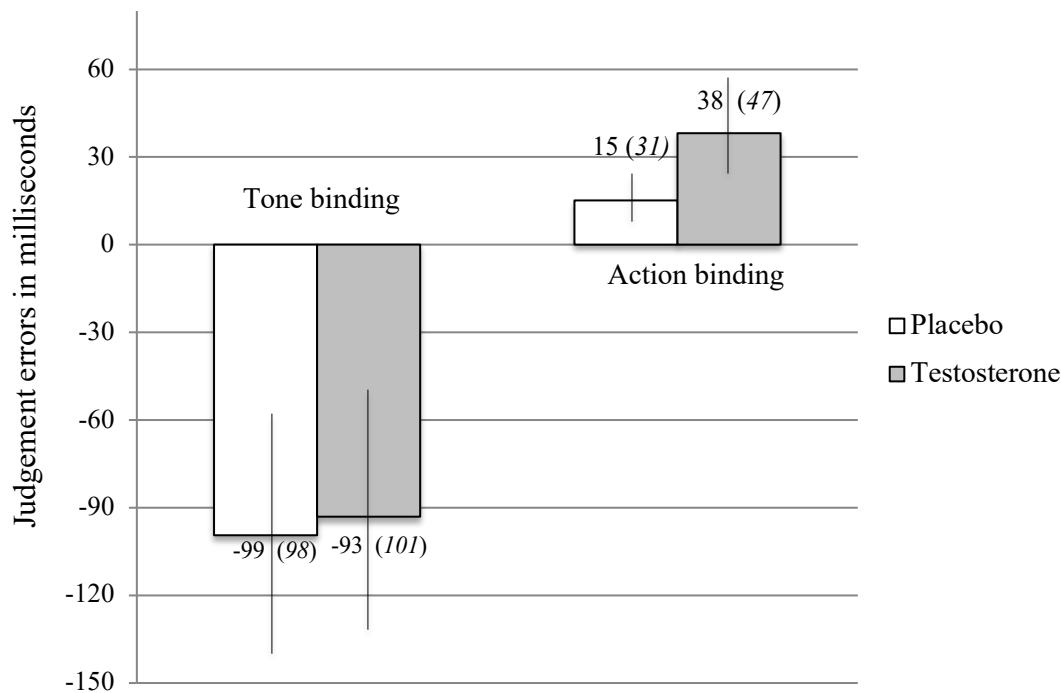
Values indicate milliseconds.

Given that the direction of shifts in temporal awareness for action and tone operant blocks (indicated by errors in time estimation) were consistent with the concept of binding, we ran one-tailed paired *t*-tests to see whether the binding effect was present. In both the placebo ($t(24) = -2.334, p = .028, d = .22$) and the testosterone conditions ($t(24) = -4.067, p = .000, d = .65$), there was a significant difference between the action baseline and action operant blocks. Significant tone binding was also found on both placebo ($t(24) = 5.027, p = .000, d = 1.09$) and testosterone testing days ($t(24) = 4.560, p = .000, d = 1.03$).

Based on a Wilcoxon signed rank test, there was no significant difference between testosterone and placebo days for global binding ($Z = -.31, p = .76, r = .06$). However, we opted for separate analyses of action and tone binding given that recent studies suggest that the two processes reflect cues that can be recruited in dissociable ways during the integration of agency (Kranick et al., 2013; Wolpe et al., 2013). Without doing so, meaningful data is lost. Differences in the effects on binding between testosterone versus placebo testing days were analyzed by assessing action binding and tone binding in two separate Wilcoxon signed rank tests. For action binding, the test indicated that binding was significantly increased

during the testosterone condition ($Mdn = 29$) compared to placebo ($Mdn = 15$), $Z = -2.32$, $p = .026$, $r = -.46$. However, no significant difference between testosterone ($Mdn = -88$) and placebo ($Mdn = -82$) was observed for tone binding $Z = -.79$, $p = .43$, $r = -.16$. For mean, instead of median values of binding scores, refer to Table 1 and Figure 2. Plots of means and individual data points on both testing days can be found in the supplementary section.

Figure 4.2. Mean binding scores for testosterone and placebo conditions.



*Note, values reflect mean scores and not median values as reported in text. SD in parentheses. Error bars reflect standard error of the mean.

We next asked whether or not the effect of testosterone on binding was specific to action binding and significantly larger than the effect on tone binding. To do this, one must run a multiple comparison test to assess whether the change in magnitude from placebo to testosterone is statistically different between action and tone binding (Nieuwenhuis, Forstmann & Wagenmakers, 2011). We therefore quantified the net increase in binding from placebo to testosterone and ran a t-test to compare the difference between action and tone binding. Although descriptively, the average increase in binding was larger for action binding ($M=23$, $SD= 50.1$) than tone ($M= -5.8$, $SD= 106.7$), due to large variance in the data,

statistically, this increase in action binding was not significantly different from the change in tone binding ($t(24) = 1.24, p = .11, d = .34$). The data therefore does not support a claim that the effect of testosterone on SoA was specific to action binding.

Looking at the placebo condition only, there were no significant correlations between 2D:4D and action ($r = .05, n = 25, p = .79$) or tone binding ($r = -.16, n = 25, p = .44$).

4.3.2 Mood data

We then investigated whether testosterone and placebo conditions differed in terms of current mood states and affective forecasting. Refer to Table 2 for descriptive statistics. We tested these variables separately using two Wilcoxon Signed-Ranks tests because they represent different constructs. That is, current mood states measured participants' feelings at the time of testing while predicted mood states involve memory and may reflect cognitive biases (Wilson & Gilbert, 2003). Not all participants provided complete sets of these data over both testing days, leaving a total sample size of 17. There was no significant difference across the two treatment conditions (placebo $Mdn = 3.11$; testosterone $Mdn = 2.90$) for positive items of the PANAS assessing *current* mood state $Z = -.36, p = .716, r = -.08$; however, scores for positive items for *future* mood state were significantly higher in the testosterone condition ($Mdn = 3.33$) compared to placebo ($Mdn = 3.11$) $Z = -2.11, p = .035, r = -.497$. No significant differences were found for negative items between the two treatment conditions, regardless of time. We then created composite PANAS scores to reflect overall positive affect for current and future moods by subtracting negative scale scores from positive scores. A two-tailed paired samples t-test indicated a significant difference between placebo and testosterone in affective forecasting ($t(16) = 3.099, p = .007, d = .61$) but not in terms of current mood states ($t(16) = .435, p = .669, d = .08$). Participants had an average score for current mood state of 1.54 ($SD = 1.17$) on the day of testosterone administration, and 1.45 ($SD = .91$) on placebo. When treated with testosterone, participants imagined a more positive future, with a mean score of 2.0 ($SD = .69$) compared to only 1.50 ($SD = .93$) when given placebo.

Finally, on the placebo day, we found no significant correlations between action binding ($r(16) = .08, p = .76$) and current mood state, nor affective forecasting ($r(16) = .03, p = .89$).

Nor were there any significant correlations between tone binding and current ($r(16) = .35, p = .17$) or future mood state ($r(16) = .39, p = .12$).

Table 4.2. Descriptive statistics for mood data

	Placebo		Testosterone	
	M	SD	M	SD
Current				
Mood				
Positive	1.33	(.85)	1.20	(.95)
Negative	1.00	(.61)	1.00	(.52)
Composite	1.45	(.91)	1.54	(1.17)
Affective				
Forecast				
Positive*	1.44	(.81)	2.43	(.71)
Negative	1.00	(.61)	1.00	(.32)
Composite*	1.5	(.93)	2	(.69)

Composite values represent overall positive affect. The asterisk indicates significant differences between testosterone and placebo testing days. Composite variables reflect overall positive affect.

4.4 Discussion

In the current study, we investigated the effect of 0.5mg testosterone on the sense of agency, as measured in terms of intentional binding. Several mechanisms have been described to explain the link between testosterone and behaviours that facilitate control over the environment (Eisenegger, Haushofer & Fehr, 2011; Terburg & van Honk, 2013). It is however unknown whether testosterone also influences more basic feelings of sensory-motor control. To the best of our knowledge, this is the first study to directly investigate the

hormonal basis of SoA and here we demonstrate a facilitation of implicit feelings of control by a 0.5mg dosage of testosterone in young women.

4.4.1 Effects of testosterone on intentional binding

Under both testosterone and placebo conditions, participants demonstrated the “intentional binding” effect. Although significant binding occurred on both testing days, confirming the validity of the task, our statistical analyses showed that action binding during the testosterone condition was significantly increased compared to placebo. However, there was no significant effect of testosterone on the magnitude of perceptual shifts for tone binding. These results suggest that testosterone facilitates the SoA, but because there was no statistically significant difference in the magnitude of change from placebo to testosterone between the two binding conditions, the current findings unfortunately have no bearing on the small but growing literature suggesting that tone and action binding are, to some extent, driven by dissociable mechanisms (Kranick et al., 2013; Wolpe et al., 2013).

Action binding was significantly increased on the testosterone-treatment day, but our data do not show any explained variance on binding for 2D:4D digit ratio (a proxy for pre-natal effects of testosterone on the brain), despite this variable explaining substantial variance in other studies involving the effects of testosterone on cognition (mind reading and social decision making) (Buskens et al., 2016; Carré et al., 2015; Montoya et al., 2013; van Honk et al., 2011). Of note, unlike these previous studies, our measure of SoA had no social component. Our findings suggest that the effect of testosterone on the SoA appears to depend on current testosterone and not pre-natal sex hormone priming in the brain (though see Olsson et al., 2016). In support of this view, studies have shown that although children with autism spectrum disorder tend to have lower 2D:4D ratios (Milne et al., 2006) – an indicator of higher prenatal testosterone exposure – they exhibit normal agency over action (David et al., 2008). Together, these findings suggest that 2D:4D digit ratios are not related to the SoA. It may therefore be the case that prenatal effects of hormones interact exclusively in tasks involving social cognition.

The modulation of SoA by testosterone is consistent with the idea that basic sensory-motor experiences of personal control may contribute toward the experience of power (Obhi, Swiderski & Brubacher, 2012). In fact, many agree that the SoA is a basic mechanism constituting the feeling of free will and self-determination (Haggard & Tsakiris, 2009;

Moore, 2016), which may have real consequences in the social sphere. Indeed, testosterone dynamics tend to be associated with personal freedom and social mobility. Karsh and Eitam (2015) have recently demonstrated that the experience of agency is desirable and rewarding in much the same way as tangible rewards, suggesting that it may function to sustain behavioral persistence even when outcomes are uncertain. An increase in SoA by testosterone may therefore explain some of the rewarding effects of testosterone (Hermans et al., 2010). The current findings therefore underscore the relationship between basic sensorimotor processes and more high-level emotional states, like those instantiated by testosterone (for e.g. social power, for review see Eisenegger et al., 2011), suggesting that mental experiences are grounded and embodied in physical experience (Barsalou, 2008; Lackoff, 2012; Varela et al., 1992). In this view, the phenomenology associated with power may derive in part from the physical and perceptual experiences of the body that are recruited during interaction.

Given that testosterone is a male-type steroid hormone and that indices of power and social dominance tend to be higher in men (Pratto, Sidanius & Levin, 2006), the current findings might be interpreted to imply that men experience increased SoA. To the best of our knowledge, no studies have focused their research question exclusively on sex differences in the SoA but one study (Caspar et al., 2017) found no effect of gender on a similar implicit measure of agency using the interval estimates procedure. However, though males have up to ten times as much circulating testosterone, females are thought to be more sensitive to the hormone (Dabbs & Dabbs, 2000), implying that different levels of testosterone can produce similar effects in men and women. Instead, differences between the sexes in terms of when and how much testosterone is released may determine the extent to which testosterone produces an effect. For instance, as with many other social contexts, testosterone response to competition differs between men and women (Kivlighan, Granger & Booth, 2005). We may therefore expect a difference in agency between men and women under these conditions, but not when simply tested at baseline.

In terms of more precise mechanisms by which testosterone has a purported effect on action binding, we can only speculate. Wolpe et al. (2012) argue that action binding increases as a function of the reliability of outcomes. Yet, in our study, reliability was consistently high, begging the question of why action binding differed across placebo and testosterone conditions? Drawing on Moore and Haggards' (2008) ideas, that the Bayesian inference

process that generates the SoA is context dependent, it may be that testosterone changes the perceived predictability of actions. For instance, if motor predictions are strong, this alone can lead to binding. Wolpe et al. (2014) argue that trait optimism, a key feature of powerful personalities (Anderson & Galinsky, 2006), predicts the exaggerated reliability of priors that predict successful perception of goal-directed action, thus explaining the “illusion of superiority” in which self-actions are perceived as being more successful than others’. Over-confidence in decision-making has been linked to narcissistic personality traits (Campbell, Goodie & Foster, 2004), which have been found to predict both intentional binding (Hascalovitz & Obi, 2015) and testosterone response (Lobbestael et al., 2014; Pfattheicher, 2016), suggesting that the effect of testosterone reported here on the SoA may be mediated, at least in part, by its influence on motor priors. Future studies will be required to test this hypothesis directly by adding a probabilistic component to the task design in which the reliability of action-outcomes is varied to directly assess the role of predictability in testosterone’s effect on agency.

What other mechanisms might account for the influence of testosterone on action binding? Mehta and Beer (2010) found that testosterone reduces activity in the orbitofrontal cortex, a region implicated in impulse control. From this perspective, impulsivity may reduce deliberation about *when* to perform an action. Indeed, Kühn and Brass (2009) have shown that deciding when *not* to act, which by default reflects the task of deciding *when* to act, is a legitimate mode of action in and of itself and recruits the same brain regions involved in deciding between a selection of actions. Thus, even though in the current design there was only one prescribed action to perform, participants had to decide when to act and would have therefore experienced some degree of response conflict. An effect of testosterone on impulsivity in response initiation may therefore help to bypass the problem of conflict.

An alternative explanation is that the increase in action binding by testosterone occurs because the action process was experienced as less effortful. Though few studies have focused on the impact of steroid hormones on the motoric system (Oki et al., 2015), Bonifazi et al. (2004) demonstrated that increased testosterone levels in a sample of men induced by the administration of human chorionic gonadotropin, reduced the threshold to evoke a motor response to TMS of the primary motor cortex. A reduction in motor threshold is thought to reflect the excitability of motor neurons (Maeda & Pascual-Leone, 2003; Ziemann, 2004), suggesting that testosterone is able to facilitate the corticospinal pathway. Increased

excitability of pyramidal neurons may therefore lead to less effortful action execution and may in turn give rise to the prospective SoA (Chambon, Sidarus & Haggard, 2013).

4.4.2 Testosterone and mood

While current mood states were not significantly influenced by testosterone, our results show that perceptions about future affective states were minimally, but significantly, more optimistic in the testosterone condition. Consistent with the null finding for current mood, previous research shows that when asked directly, participants administered testosterone fail to reliably report any changes in affect (Eisenegger et al., 2010). However, affective forecasts may involve cognitive biases and here they were found to be more positive on the testosterone day than on placebo.

Several studies indicate that optimism is, in fact, linked to the perception of control (Darvill & Johnson, 1991; Fontaine, Manstead & Wagner, 1993; Guarrera & Williams, 1987; McKenna, 1993). For instance, powerful individuals tend to believe more than others that they have control over their futures (Guinote, Brown & Fiske, 2006; Heine et al., 1999; Lachman & Weaver, 1998). Of note, we did not find a relationship between binding scores and predictions about future affect. This implies distinct mechanisms underpinning the effect of testosterone on agency and future affect. For instance, Markowitsch and Staniloiu (2010) have proposed that, with respect to memory processing, which is recruited when forecasting the future (Schacter et al., 2012), the amygdala functions to bias cues so that encoded events of a particular emotional significance can be successfully searched for and reactivated. Given that testosterone is known to activate the amygdala (see Heany et al., 2015 for review) and facilitate social approach behaviour (Radke et al., 2015), this suggests a mechanism via which salience is attached to more positive memories in response to testosterone administration. Enhanced activation of the amygdala may therefore mediate the effects of testosterone on positive perceptions of future affect, an idea corroborated by evidence linking the amygdala to optimistic thinking (Sharot et al., 2007) and testosterone to enhanced self-efficacy (Costa, Serrana & Salvador, 2016) and could be tested directly in future imaging studies by comparing recall of positive versus negative autobiographical details in testosterone-treated participants. Together with the finding of increased SoA, these results suggest that testosterone might also support the early, prospective sense of agency which is especially important in threatening or ambiguous social settings, like competition, where a proactive response may be advantageous.

4.4.3 Limitations

There are several limitations to the current research which should be addressed in future replication studies. We were not able to assess salivary or plasma levels of testosterone. However, based on previous studies that demonstrate a ten-fold increase in women's circulating testosterone in response to 0.5mg of the hormone (Tuiten et al., 2000), we can infer with a reasonable degree of confidence that the significant increase in action binding that was seen on testosterone-treatment days was an effect of the administration, given that all other variables were held constant. Secondly, although we counter-balanced action versus tone conditions across participants and between testing days, we did not counter-balance baseline and agency blocks. Even so, our intentional binding scores on placebo days are comparable to other studies (Moore et al., 2012; Kranick et al., 2013) and we surmise that because a significant difference arose between placebo and testosterone days in action binding, this effect is unlikely simply accounted for by order.

Finally, it will be worthwhile to probe alternative measures of implicit SoA (e.g. sensory attenuation) but also explicit, meta-cognitive ratings of agentic experience. Ultimately, the investigation into how testosterone modulates the SoA in social contexts will offer information that is most ecologically useful. In the social world, where authorship is often ambiguous (de Bézenac et al., 2015; Pacherie, 2013) the SoA may play an important role in the feeling of responsibility and achievement, which may translate into an experience of power.

4.4.4 Conclusion

To conclude, this study shows that 0.5mg of testosterone enhances the implicit sense of agency and induces the perception of a brighter future. We found this significant effect of testosterone on SoA exclusively for action binding, and not tone binding. Because intentional binding on placebo did not predict positivity in affective forecasting, it appears that testosterone influences SoA and optimism via distinctive brain mechanisms. Although our effects sizes were modest, the pattern of results reported here contributes to the literature on the embodiment of social power and highlights an important link between testosterone

and the experience of control. That is, feelings of agency associated with power and assertiveness may emerge out of more basic sensorimotor processes linked to control over the body. This rudimentary form of empowerment may constitute a key mechanism by which testosterone-fuelled dominance is initially achieved.

Chapter 5 | General Discussion

This thesis began with a discussion of power, the notion that being powerful is about having *capacity*: to be goal-directed and defensively independent, free from the controlling wills of others. More simply, this freedom is about action and action is the domain of the body. As proposed by Merleau-Ponty (1945), “*my body appears to me as an attitude directed towards a certain existing or possible task*”. In the social domain, thinking about power, that ‘task’ may take the form, implicitly, of ‘the other’, conceivable in terms of the potential range of actions and sensations given to us by our embodiment. Indeed, there is now a great deal of evidence showing that social factors and emotional states influence embodiment and vice versa (Banakou, Grote & Slater, 2013; Durlak & Tsakiris, 2014; Izjerman et al., 2012; Maister et al., 2013; Moeini-Jazani et al., 2017; Paton et al., 2012; Pfister et al., 2014). The embodied cognition framework thus offers a novel methodology for studying some of the rudimentary processes that might support the attainment of social power. Here I have begun to explore the general hypothesis that power is embedded in the owning and control of a body – one’s own body. No studies to date have explored a potential role for testosterone in the relationship between sensorimotor mechanisms and social power. This is an important question since testosterone, a male-type hormone, is well known for its role in physical power but also social power. Thus, as a first step toward answering this question, using a pharmacological manipulation paradigm, I have tested whether a 0.5mg dosage of testosterone influences three processes of embodiment. This thesis was informed hypothetically but is exploratory in nature. It has answered some questions but posed many more.

Findings can be summarised as follows: In experiment one, testosterone was found to increase interoceptive accuracy (IAcc). Following ostracism, however, this advantage in processing was lost. In this experiment, better IAcc was negatively correlated with trait anger. In experiment two, during the Rubber Hand Illusion, a drop in limb temperature in participants’ own hand only occurred in the placebo group. There were no further effects of testosterone on other indices of the RHI, such as subjective ownership or proprioceptive drift. In this experiment, proprioceptive drift was positively related to overall mood disturbance and a positive relationship between temperature decline and subjective ownership emerged. Finally, in experiment three, testosterone was found to increase the

implicit sense of agency, as measured using an intentional binding task, though this effect was specific to action binding. In this experiment, testosterone also lead to an optimism bias in thinking about the future.

5.1 Coherence among experimental findings

In experiment one, the effects of testosterone on interoceptive accuracy were explored in a sample of young women. Interoceptive accuracy (IAcc) refers to the precision with which one is able to detect internal physiological signals (Cameron, 2001; Craig, 2002) and in this experiment we utilized a commonly employed procedure, the heartbeat tracking task (Schandry, 1981), to measure this construct. Testosterone was found to increase IAcc at baseline, that is, prior to any social manipulation. This finding contributes to the growing literature showing that interoceptive acuity is influenced by state variables, and is not only a static, trait-like ability (Ainley et al., 2013; Durlík, Brown & Tsakiris, 2014; Durlík & Tsakiris, 2015; Fairclough & Goodwin, 2007; Herbert et al., 2012; Koroboki et al., 2010). The implications of increased IAcc by testosterone are speculative, but based on prior literature, I have proposed that increased IAcc at baseline may be interpreted in the same way as *trait* IAcc. In other words, people who generally have high levels of circulating testosterone may be considered to have high trait IAcc. This may shed light on one mechanism via which elevated testosterone manifests its power-promoting effects. For example, Pollatos et al. (2015) have suggested that the ability to differentiate variations in bodily responses may contribute to the feeling of increased control.

This perspective conflicts, however, with other research showing that people with more anxiety tend to have higher IAcc (Domschke et al., 2010; Terasawa et al., 2013). What's more, is that self-report measures of dominance did not correlate with IAcc in the placebo group – but, trait dominance may depend on low cortisol as well (Terburg, Morgan & van Honk, 2009; van der Westhuizen & Solms, 2015b). Of note though, studies have found that while testosterone is able to reduce responses to unconsciously processed fear, consciously experienced anxiety is not necessarily affected by the hormone, suggesting that the coping benefits of high IAcc may similarly occur outside of conscious awareness. For instance, interoceptive awareness is considered the core channel via which “gut feelings” are perceived (Dunn et al., 2010), and therefore acuity may confer several benefits to cost/benefit judgement in ways that are not consciously apparent. Better IAcc is thought to improve

predictive models of sensory self-monitoring (Brass & Haggard, 2010; Tsakiris, Tajadura-Jiménez & Constantini, 2011) and in this way support decision-making and goal-directedness. Moeni-Jazani et al., (2017) further argue that high IAcc may account for the enhanced self-focus characteristic of socially powerful people. Thus, a role for testosterone in linking constructs of “the powerful” with embodiment may be explained in part by the mechanism of interoceptive awareness.

Quartrocki and Friston (2014) propose that attention directed toward the internal milieu may come at the expense of attuning to other’s externally perceived needs. This has been proposed as one mechanism via which powerful people maintain their own agendas. However, some have suggested instead that being a good empathizer depends on *elevated* IAcc (Ernst, Northoff, et al., 2013; Fukushima et al., 2011). This would be at odds with the current finding of improved IAcc in the testosterone group, since the hormone is often linked to impoverished empathic ability (Hermans et al., 2008; Montoya et al., 2013). The interoception/ultraism argument is based on findings that individuals with high IAcc tend to display more facial mimicry, thought to be a basic embodied mechanism of affect-sharing (Ainley, Brass & Tsakiris, 2014) and that a critical component of empathy, which IAcc may assist in, is the ability to differentiate between the self and other (Colonnello et al., 2013; Decety & Sommerville, 2003). However, studies in embodiment have shown that there are many ways to represent the self and the other (Haggard, Taylor-Clarke & Kennett, 2003; Jeannerod, 2004; Tsakiris, Schutz-Bosbach & Gallagher, 2007; Uddin et al., 2007) and the key to empathizing may involve affect sharing (Singer & Lamm, 2009) or depend on an as-yet, unidentified critical balance. For instance, Fotopoulou and Tsakiris (2017) have proposed that empathy may require “good-enough” interoceptive processing, but that high acuity is not the critical variable. This may explain why IAcc was not found here to correlate with Caring as a personality trait, a construct which does not necessarily take into account self/other distinction. That IAcc might assist in mentalisation but not empathy, *per se* (Ainley, Maister & Tsakiris, 2015), is also consistent with data showing that testosterone can, under certain conditions, encourage certain forms of socially astute behaviours too. The pro-social behaviours linked to testosterone tend to be those which involve some degree of representation of the other, *in relation* to the self (social/economic trade-offs, Boksem et al., 2013; Dreher et al., 2016; Eisenegger et al., 2010), and high IAcc in its inherently self-specifying nature (Legrand & Ruby, 2009), may help to monitor the distribution of value between self and other in these social contexts.

The finding of elevated IAcc by testosterone administration compared to placebo is in keeping with data from experiment three, that testosterone increased the implicit sense of agency (SoA), as measured by the intentional binding task (Moore & Fletcher, 2012). Support for common mechanisms underpinning the two processes comes from imaging studies: activity in the insula cortex, which consistently associates with interoceptive awareness (Craig, 2002; Critchley et al., 2004; Wiebking et al., 2014) and the sense of agency (Farrer & Frith, 2002; Farrer et al., 2003; Sperduti et al., 2011), is a brain structure known to be activated by testosterone (Banczerowski et al., 2001; Bos et al., 2010; Heany et al., 2015; Lentini et al., 2013). This link is further based on findings by Ainley (2015) who report a positive relationship between IAcc and intentional binding. However, this link was driven by effect binding and not action binding and here testosterone was only found to enhance action-binding. Contemporary theoretical perspectives on action suggest that movement is coded in terms of its sensory consequences (Friston, 2009; Hommel, 2009; Schütz- Bosbach & Prinz, 2007). Unlike exteroceptive effects, presumably indexed more accurately by tone binding (Waszak et al., 2012), interoceptive awareness may assist in predicting anticipated bodily reverberations of voluntary actions to enhance the SoA in line with the ‘cue integration’ theory (Moore et al., 2009; Moore and Fletcher, 2012), which states that the reliability of information in determining matches between external events and predictions made about the effects of a voluntary action is what leads to the feeling of control. However, pressing a computer button does not likely produce a very robust ‘visceral image’ and thus the failure of Ainley (2015) to find a link between action binding and IAcc suggests that effects of testosterone on the heart and body (Nieschlag, Behre & Nieschlag, 2012; Tambo, Roshan & Pace, 2016) might interact with interoceptive processing to represent and predict the interoceptive effects of action. It was proposed earlier that testosterone may facilitate action binding by increasing the perceived predictability of actions, and this predictability may relate to interoceptive effects, exclusively. Nonetheless, given that Ainley (2015) report an association between IAcc and tone but not action binding, it is possible that testosterone influences interoception and the SoA via divergent mechanisms. It will be important for future investigations of the SoA to examine the specific role of interoceptive *predictions* and interoceptive *effects* of actions given that most work to date has focused on exteroceptive effects of actions, even though action evolved to respond to the visceral needs of the organism (Damasio, 2010; Panksepp & Biven, 2012).

If testosterone does interact with IAcc to influence the SoA, improved, anticipatory body signalling may also have the effect of encouraging “approach”-related thoughts or feelings about the future, a common trait seen in the powerful (Fast et al., 2012; Guinote, 2017; Hofstede et al., 2002) and those with high testosterone (Radke et al., 2015; Terburg et al., 2012). For instance, Penton et al. (2014) showed that interoceptive sensitivity positively relates to attributional styles characterized by perceived control. The finding here of elevated IAcc by testosterone as well as enhanced optimism by testosterone in experiment three, is consistent with this link.

Elevated IAcc following testosterone administration also aligns with the main finding from experiment two, that a single dosage of testosterone compared to placebo inhibited a drop in limb temperature following induction of the Rubber Hand Illusion (RHI). Although conjecture, one might expect improved interoceptive awareness in individuals who exhibit more *resistance* toward homeostatic dysregulation. According to Pennebaker and Lightner’s (1980) ‘competition of cues’ hypothesis, exteroceptive and interoceptive stimuli continuously compete for the organism’s limited attentional resources. Those participants more strongly influenced at the homeostatic level by top-down, *body-as-object* beliefs may in turn experience themselves to a lesser degree as *body-as-subject*, with correspondingly poorer IAcc. This finding is consistent with Tsakiris et al., (2011) who found that better IAcc was associated with less proprioceptive drift and less temperature drop in the participants’ real hands during the RHI. These authors argue that more acutely attuned interoception might facilitate efficiency in the processing of body-related percepts. It is therefore somewhat surprising that testosterone had no effect on proprioceptive representations. Nonetheless, given the importance of interoception for the integration of somatosensory and visceral information, as well as for higher-level representations of the self (Suzuki et al., 2013), IAcc may reflect a critical process in the physiological regulation of the bodily self. This raises the possibility that testosterone inhibits the extent to which representations of the bodily self – or the “body matrix” (Mosely et al., 2012) – are able to stray from the boundaries demarcated by the physical body, a mechanism that might involve interoceptive precision (Ainley et al., 2016). Future models specified according to the principals of predictive coding may prove valuable in explaining this process as well as how the body matrix in its relation to interoception might come to *direct* homeostatic investment? From the perspective of Bayesian processing (Friston, 2010), this process might operate in similar ways to perception and action of the body in the external world – that homeostatic investment

moves just as the body would, via the testing of predictions (Friston, Mattout & Kilner, 2011), which in such case would involve interoceptive and not proprioceptive predictions. I will return to this issue of how the body matrix might direct homeostatic regulation in due course.

To summarize this section, in relation to existing literature, there are a number of consistencies in the effects of testosterone on interoceptive accuracy in its relationship to body ownership and the SoA. However, the nuanced effects of the hormone on embodiment – i.e. no effect on proprioception or subjective ownership in the RHI nor on tone binding in experiment three – contribute to the argument that indices of the RHI may be dissociable (Cowie et al., 2013; Rhode, Luca & Ernst, 2011), as might be the case with action and tone binding in studies of the SoA (Kranick et al., 2013; Wolpe et al., 2013). The distinct effects of testosterone may help to shed light on these dissociations. For example, testosterone via its modulation of the motor and muscular systems (Maeda & Pascual-Leone, 2003; Sinervo, et al., 2000; Sinneasael et al., 2011; Ziemann, 2004) might preferentially modulate aspects of embodiment that relate to action. The following section will explore some of the implications of this idea.

5.2 Testosterone, embodiment and action

The findings reported in this thesis provide some support for the view that testosterone enables the acquisition of power by influencing embodiment processes that support action. In experiment two – the Rubber Hand Illusion, – although the groups did not differ in terms of the extent to which they subjectively felt ownership over the rubber hand, nor the amount of proprioceptive mislocation, only the placebo group displayed a significant drop in limb temperature in their own hand following induction of the illusion. As stated in chapter three, this effect by testosterone was interpreted to show that effective maintenance of the body's representational boundaries can be regarded, conceptually, as a defensive state facilitating the integrity of the self. Thus, much like holding one's ground in response to territorial intrusion in those with high testosterone (Neave & Wolfson, 2003), homeostatic boundaries in the hormone-treated group were less vulnerable to change. This suggests that testosterone monitors the body much like it would monitor territory and status.

In essence, the illusion presents a threat to the integrity of the bodily self, but also the *active* self, based on findings that high levels of identification with a foreign body during multisensory illusions leads not only to actual reduced motor potential (Della Gatta et al., 2016) but also conformity behaviour (Paladino et al., 2013). Though the *body-as-object* and self-localization in space are two important facets of bodily representation, they may be less relevant for the experience of social power with its intimate ties to action. As outlined in the introductory chapter, the intentions and plans of powerful individuals tend to be chronically available, enabling conception of the self as an active self to support an approach-orientation (Guinote, 2010, 2017). Higher interoceptive awareness, for example, may play a role given that the fundamental basis of action and its systems of control is to fulfil the organism's homeostatic needs as signalled via interoception (Craig, 2010; Damasio, 2010). Explicit body representations as assessed using self-report measures in RHI may be less centrally involved in "approach".

Firstly, though subjective feelings of objective body ownership have been shown to successfully recruit the brain's defensive system (Armel & Ramachandran, 2003; Ehrsson et al., 2007) and may in this way act as a mechanism via which a phenomenology of territoriality over external objects manifests, the exteroceptive self is the self *objectified* and may have less role to play in orchestrating action plans. Self-objectification is linked to outward attention to the body's appearance which may come at a cost to subjective experience of the body's effectiveness (Ainley & Tsakiris, 2013; Fredrickson & Roberts, 1997; Ainley). Secondly, with regard to proprioceptive drift, although correct proprioception is necessary for accurate motor commands (Graziano & Botvinick, 1999), action may be immune to visual illusions (Aglioti, DeSouza & Goodale, 1995). Kammers et al. (2008) found that during the RHI, there were no significant disturbances to kinematic parameters of motor responses. They argue therefore that proprioceptive mislocalisation within the context of the RHI occurs as a result of visual capture in perceptual processing, that alternations of proprioceptive information by the visual illusion only occurs for the perceptual task, not for motor tasks. Thus, because proprioceptive drift in the RHI does not necessarily have meaningful bearing on action, this may account for its lack of modulation by elevated testosterone.

Instead, physiological regulation in response to changes in perceived body ownership may have downstream effects for action opportunities. Not only has cooling of the real hand been

demonstrated several times (Hohwy & Paton, 2010; Kammers, Rose & Haggard, 2011; Moseley et al., 2008; Thakkar, Nichols, McIntosh & Park, 2011; Tsakiris, Tajadura-Jiménez & Constantini, 2011; Van Stralen et al., 2014), but della Gatta et al., (2016) have shown that motor evoked potentials in the real hand decreases significantly following induction of the illusion. This implies that a stronger voluntary command would be necessary to evoke a motor response, indicating that action potential in the real limb is decreased following identification with the prosthesis. Whether or not this kind of physiological dysregulation corresponds to a drop in limb temperature has not yet been formally established, but one might expect this to be the case given that several studies have shown motor and sensory nerve conductivity and responsivity to decline in response to cooling (Abramson et al., 1966; Dioszeghy & Stalberg, 1992; Halar, DeLisa & Soine, 1983; Herrera et al., 2010). Motor interference of this kind may function to regulate approach-avoidant / dominant-submissive behaviour. For instance, animal models of social defeat show reduced activity in motor and motivational brain regions and general declines in behavioural output (Stone et al., 2007). If temperature changes and motor evoked potentials have a shared mechanism in the RHI, the finding here that testosterone inhibits a temperature drop could be taken to reflect an embodied mechanism via which the hormone regulates approach mechanisms. Similar multi-sensory integration processes instantiated by the motor neuron network (Fadiga, Craighero & Olivier, 2005; Rizzolatti, 1995) may occur in naturalistic settings, exerting subtler but comparable effects.

A role for embodiment processes in testosterone's effects on "approach" behaviour is further supported by the finding from experiment three, that testosterone increased action-binding, an implicit measure of sensory-motor agency. The sense of agency (SoA) is thought to be a fundamental process underlying the experience of free will, and is argued to sustain motivation in goal-pursuit by virtue of being rewarding in and of itself (Karsh & Eitam, 2015). Moreover, Gentsch and Synofzik (2014) have suggested that cue weighting during the sensory-integration process may be influenced by activated self-motives, implying that those with strong agendas experience a stronger SoA. Minohara et al. (2016) recently showed that the strength of an intention positively predicted the sense of agency. Strong motives, as expected to be seen in those who are optimistic (Carver & Scheier, 2014; Nes, Evans & Segerstrom, 2009), shown here to arise when testosterone levels are high, may have the effect of strengthening the perceived predictability of actions. For example, Wolpe et al. (2014) show that trait optimism predicts the exaggerated reliability of action priors, which

appears to be linked to action binding. I have proposed earlier that testosterone may enhance action binding by strengthening motor predictions. This may be achieved, in conjunction with strong intent, by sufficient activity in motor representations of the body, shown by Della Gatta et al. (2016) to be reduced in the RHI in response to subjective ownership over the rubber limb. Since testosterone appears to assist in the maintenance of physiological regulation under conditions of multisensory integration, up-regulation of signals involved in the normal functioning of acting limbs may account for its ability to facilitate action binding.

These alleged effects of testosterone on bodily representations that support action may form the basis of a phenomenology of power. It has already been proposed that the body is given to us as a source or power for action (Gallese & Sinigaglia, 2010), and this action potential may inform the subjective sense of power.

5.3 A phenomenology of power

From the perspective of embodied phenomenology (Merleau-Ponty, 1945), since we draw on the body to understand ourselves and the world around us, bodily signals of all kinds constrain experience, even when these signals are outside of conscious awareness (Gallagher & Aguda, 2015). Thus, because bodily signals are critical in the regulation of adaptive, ongoing behaviour, the state of the body should meaningfully interact with cognition and emotion. For instance, Duclos et al., (1989) and Stepper and Strack (1993) found that emotional body postures have the capacity to induce corresponding affective states. Simply activating the muscles to form a clenched fist appears to elicit the concept of power (Schubert, 2004; Schubert & Koole, 2009) and even encourage “approach” (Tops & de Jong, 2006). This suggests that there are peripheral feedback mechanisms that influence subjective state and similar associations have been reported in body illusions. Kállai et al. (2015) found that proprioceptive mislocalisation and subjective ownership in the RHI was stronger in people who scored higher on measures of harm avoidance and interpersonal sensitivity, respectively. Findings from experiment two are consistent with this view: larger errors in proprioceptive drift were related to increases in mood disturbance. In experiment one it was found that individuals higher in dispositional rage scored lower in heartbeat tracking ability. These preliminary findings do not demonstrate a causal role for the body in the experience of specific emotion states but they do suggest that negative emotions are linked to disembodiment.

The collective findings from this thesis suggest that testosterone might contribute to an embodied phenomenology of power in two main ways. Power implies feeling powerful but also recognising when power is interrupted. Testosterone may thus contribute toward “effort sense” and secondly, it may modulate the conscious availability of bodily percepts to encourage defence.

5.3.1 Effort sense

The term “effort sense” is envisioned as a feeling of capacity to act. Via its regulatory effects on physiological embodiment as demonstrated in the RHI, testosterone may help to maintain adequacy of bodily resources and in this way support “approach” mentality in situations where physiological investment becomes unstable (see for e.g. Izjerman et al., 2012). Mosely et al. (2008) have suggested that cooling during the RHI reflects a disturbance in conception of the bodily self and that higher-order beliefs about the external, bodily self therefore appear to be capable of modulating homeostatic investment in the body. Though these authors argue that it is the higher-order belief that drives thermal dysregulation, there may be downstream consequences for mental experience. Indeed, Kammers et al. (2011) found that cooling a participant’s hand prior to induction of the RHI had the effect of increasing feelings of subjective ownership.

In relation to body temperature, lowered skin temperatures are associated with decreases in metabolism (Landsberg et al., 2009), that is, less generation of energy. Because fatigue is known to modulate mental experience, such as making distances appear further away (Witt & Proffitt, 2008), the availability of energy should be psychologically empowering (“Energy is delight” Panksepp, 1998, p. 136). Several findings support the idea that activation of the motor system, for instance, has downstream consequences for the experience of power. Activating the muscles through bodily gestures, like making a fist, has the effect of making men feel powerful (Schubert & Koole, 2009). Briñol et al. (2009) found that participants who performed self-evaluations in dominant-open compared to constricted-submissive postures, appraised their evaluations with greater confidence. Cooling of the body on the other hand, has been linked to reduced motor potential (Abramson et al., 1966; Dioszeghy & Stalberg, 1992; Halar, DeLisa & Soine, 1983; Herrera et al., 2010) and aversive emotional states (Boudewyns, 1976; Bugental & Cortez, 1998; McFarland, 1985; Mittleman & Wolff,

1939; Or & Duffy, 2007; Rimm-Kaufman & Kagan, 1996; Zhai & Barreto, 2006). Cooling might engender part of what it feels like to be anxious. Specifically, in response to anxiety, sympathetic-driven vasoconstriction appears to underlie the rapid, short-term drop in skin temperature as a means to increase core body temperature (Oka, Oka & Hori, 2001). A portion of thermosensitive neurons within the pre-optic area of the anterior hypothalamus (Hori et al., 1986) – an area strongly implicated in the expression of testosterone-mediated dominance behaviour (for review see van der Westhuizen & Solms, 2015) – are known to respond to emotionally arousing stimuli, and in this way psychological factors are linked to temperature changes.

With reference to experiment three, Demanet et al. (2013) have proposed that the sensation of effort is a critical cue used by the brain to generate a sense of agency. In their study, the authors found that increasing effort lead to a corresponding increase in intentional binding, a finding which appeared to be driven by action binding specifically. Importantly though, the contribution of effort sense to agency appears to be abolished when effort becomes straining (Howard, Edward & Bayliss, 2016). Thus, it is possible that an effect of testosterone on action binding was mediated by its ability to modulate the sensation of effort, possibly via other embodied channels related to physiological regulation. For instance, a recent study has shown that low testosterone depresses central neural drive to the body's muscles, suggesting that elevated testosterone might increase excitability of the entire neuromuscular system (Felici et al., 2015). Whatever the mechanism, feeling agency is, in and of itself, a subjective sense of having *influenced*, meaning that it must contribute in some way to a phenomenology of power, in the most rudimentary sense of the word. For example, Obhi et al., 2012 found that making participants feel powerless had the effect of reducing implicit feelings of sensorimotor agency.

The idea that testosterone may inform a phenomenology of power in this way is endorsed by animal models of dominance. Zhou et al. (2017) argue that brain mechanisms involved in effort-based decision-making may constitute the neurobiological substrate of competitive drive and perseverance.

That testosterone might improve accuracy in the conscious perception of cardiovascular signals, further supports the perspective that it influences the sense of effort, even though this influence might be implicit. For instance, access to bodily or “gut feelings” (Dunn et al.,

2010) and the fluency of cognitive operations that high IAcc is argued to afford, may be used to infer levels of control (Pollatos et al., 2015). Indeed, Moeini-Jazani et al., (2017) recently showed that IAcc was increased by placing participants in a high-powered social position. In line with the role of interoception in homeostasis, Declerck et al. (2006) have proposed that the perception of control emerges from the brain's ability for self-regulation, which enables flexible, goal-focused behaviour and high IAcc is regularly linked to emotional regulation (Füstös et al., 2012; Kever et al., 2015; Werner et al., 2013). Cook and Beaven (2013) have further argued that the gainful effects of testosterone on performance may have to do with its ability to signal effort and the readiness to act, a function that may depend crucially on interoceptive processing. However, a role for IAcc in effort sense is at odds with findings from the Cyberball manipulation in the testosterone group. For effort sense to decline in threatening situations exactly when it might be most advantageous for power motives suggests that it might be less related to interoceptive accuracy than initially proposed. Instead, accuracy in interoceptive processing – but not interoceptive percepts themselves - might be more closely linked to cognitive inferences of control.

5.3.2 Simulating embodied loss

Because accuracy requires conscious access to interoceptive representations, a second channel via which testosterone might regulate power is by simulating a loss of bodily feedback to convey when power is interrupted.

The second main finding of experiment one was that individuals who received testosterone compared to placebo exhibited a decline in performance on the heartbeat tracking task immediately following rejection in the online Cyber ball game. Though both groups rated their subjective experience similarly, this finding suggests that elevated testosterone does not make one immune to the implicitly distressing reality of being socially ostracized but rather, that testosterone sensitized participants to signs of social threat. This interpretation is in keeping with studies that show strong activation of the amygdala in response to testosterone (Bos et al., 2010; Hermans et al., 2008; Radke et al., 2015; van Wingen et al., 2009) and that it reflexively prolongs gaze to angry, threatening faces (Terurg et al., 2011).

A transient loss in interoceptive accuracy does not necessarily imply dysregulation of the body. Interoceptive inference has been hypothesised to function according to Bayesian

predictive coding models (Pezzulo, Rigoli & Friston, 2015). Because allostatic control must overcome a *distal temporal relation* (it takes time for homeostatic demands to be restored), interoceptive representations reflect predictions to anticipate, ahead of time, homeostatic needs. Thus, a loss in visceral awareness is not immediately critical, unlike an actual loss in physiological functioning (eg. Thermal changes). Possibly then, visceral awareness can be temporarily exploited to serve communicatory needs.

I have proposed earlier that a decline in IAcc may reflect a shift in attention and function phenomenologically to transiently embody loss. A shift in processing, externally, toward the *other* may explain how testosterone prolongs dominant gaze (Terburg et al., 2011) and promotes vigilance toward cues of social threat (Goetz et al., 2014; van Honk et al., 2001). That the modulation of IAcc might have a communicatory function too is an interpretation that emerged from findings from Durlak and Tsakiris (2015), who showed that IAcc drops in response to social ostracism. These authors have proposed that an outward shift in attention might reflect activation of the brain's reactive control system (Tops et al., 2010), which tends to operate under conditions of rapid change and unpredictability. However, in line with phenomenological theories (Merleau-Ponty, 1945), it should also *feel like something* when this control system is active. Though unexpected stimuli can be good or bad, Fairclough and Goodman (2007) have observed decline in IAcc following exposure to stress. Low acuity in interoceptive awareness has also been linked to unpleasant emotional states (Avery et al., 2014; Haas et al., 2016; Paulus & Stein, 2006; Werner et al., 2013) and trouble with decision-making (Dunn et al., 2010), possibly impinging on the subjective sense of control (Pollatos, Matthias & Keller, 2015). Possibly, loss in interoceptive sense is equally as dysregulating as loss in exteroceptive sense. In experiment one, it was found that individuals higher in dispositional rage scored lower in heartbeat tracking ability. Rising levels of testosterone have also been linked to feelings of anger in response to provocation, (Peterson & Harmon-Jones, 2012), but the relationship of testosterone to aggression appears to depend on contextual variables (Chen, Raine & Granger, 2018). This underscores a proposed link between lowered IAcc and the interruption of control and may explain why testosterone is also associated with reactive aggression and brain changes associated with this state (Hermans et al., 2008; Mehta & Beer, 2010).

The proposal that a decline in IAcc has a functional role related to threat signalling remains speculative due to insufficient empirical data. Interoceptive accuracy is regarded by many to

be a trait variable because attempts to alter it have been met with challenge (Khalsa et al., 2008; Parkin et al., 2014). Moreover, Garfinkel et al., (2014) have shown that social threat signalling is enhanced by interoceptive processing. Transient decrease in IAcc in the testosterone group following social ostracism may therefore reflect a process via which the hormone is able to suppress the conscious recognition of threatening stimuli (van Honk & Schutter). Furthermore, two studies have shown that testosterone declines following Cyberball rejection (Radke et al., 2017; Seidel et al., 2013). Thus, the advantage to IAcc in the testosterone group may have simply been abolished due to falling levels of the hormone. But if so, why was a corresponding decline in IAcc not also observed in the placebo group? Tentatively, since testosterone is certainly not the only mechanism able to influence IAcc (Ainley et al., 2013; Herbert et al., 2012), that the placebo group did not show a decline in IAcc as well, might imply a basement effect – testosterone may offer an advantage to IAcc, but if it falls below a baseline threshold, may cease to exert an influence. Nonetheless, the more straightforward answer might be that the placebo group simply did not perceive rejection in Cyberball as a genuine threat.

Future studies will benefit the field by investigating the behavioural and affective ramifications of changes in interoceptive acuity in emotional contexts, but also, most importantly, the time course of these changes. For instance, if a drop in IAcc is only transient, this would support its role in loss communication without impacting negatively on coping and adaptive behaviour. If IAcc remains lowered in testosterone-treated individuals, IAcc as a possible mechanism underpinning the acquisition of power will have to be revisited. It will be important to determine too, if declines in IAcc following threat are contingent on specific personality/biochemical factors.

5.4 Interoceptive precision versus immune regulation of the self

The findings that testosterone 1) upregulates conscious perception of internal bodily signals, 2) preserves homeostatic investment in the body and 3) promotes action-effect relationships, might be taken to suggest that testosterone may exert the generalized effect of promoting a brain-body connection, possibly via its ability to increase the precision of interoceptive priors (Ainley et al., 2016). For instance, increased attention to bottom-up signals may explain why testosterone also modulates the sense of agency (more accurate prediction of the effects of actions that occur within the body, i.e. When I achieve my goal, my body

should feel *like this*). In the body ownership domain, precise prediction errors may serve to anchor the self to the body (Ainley, 2015). However, whether an effect of testosterone on anchoring to the body would derive from central brain mechanisms (e.g. Interoceptive predictions via insula representation or via the hormone's direct effects on the body, that is, more precise prediction errors due to stronger body functions) is not yet clear. Though presumably, the two channels interact. As I have proposed earlier, physically rewarding effects of testosterone on the body may increase priors about the importance of bodily afferents and in that way increase precision of interoceptive prediction errors. Nevertheless, there are some caveats to this argument. Firstly, the effect of testosterone on IAcc was context-dependent. After social ostracism, no benefit to interoceptive acuity was observed. This suggests that testosterone may encourage iterative cycling between perceptual and active inference. For example, in experiment one, at baseline, IAcc in the testosterone group was better, implying perceptual inference. However, under a condition of threat, this advantage was lost, suggesting a shift toward active inference which has the effect of decreasing interoceptive precision but encouraging action. In keeping with a self-regulatory account of power and testosterone, according to Farb et al. (2015), flexibility in precision and inferential styles may be a marker of adaptive behaviour.

As a second caveat against the simple explanation of interoceptive precision, testosterone did not decrease ratings of subjective identification with the rubber hand in the RHI study, as would be expected if interoceptive prediction was a primary mechanism via which the hormone affects embodiment. For instance, Tsakiris, Tajadura-Jiménez and Constantini (2011) found that high IAcc predicted lowered ratings of subjective ownership with the rubber hand. Nor did testosterone provide any advantage to proprioceptive representation, which is argued by some to form part of the interoceptive system (Ádám, 2010; Cameron, 2002). In experiment two, proprioceptive drift in response to the illusion was comparable across placebo and hormone groups, suggesting that testosterone provides a very specific advantage to bodily representation. Testosterone's effect on bodily representation might derive largely from peripheral action.

This proposal is highly speculative and founded on just a single finding from this work, but it is based on fascinating new ideas about multi-sensory integration, body ownership and the immune system (Constantini, 2014). At the biological level, the immune system is the chief regulator of me-versus-not-me entities. Damasio (2003) has even suggested that the best

conception of the self is where the immune system takes the self to be. As shown by Barnsley et al. (2011), disownership of the real limb in the RHI is reflected by increased histamine reactivity in the hand, an immune reaction to foreign bodies. In general though, pro-inflammatory cytokines take on the task of flagging foreign or invading molecules and in some cases, the immune system can turn on the host to attack its own cells, as in the case of autoimmune diseases (Blanco et al., 2008; Gee et al., 2009). Of relevance here is that testosterone is a well-known suppressor of pro-inflammatory cytokines in both health and disease (Corcoran et al., 2010; D'Agostino et al., 1999; Hatakeyama et al., 2002; Kanda, Tsuchida & Tamaki, 1996; Maggio et al., 2006; Malkin et al., 2004; Olsen & Kovacs, 1995; Traish, Saad & Guay, 2009; Yesilova et al., 2000). What this means is that testosterone appears to facilitate identification of one's *own* body at the cellular level, helping to keep the immune system in-check from turning on self-cells – a form of self/other distinction, but also *self-regulation*. Thus, it is possible that the failure of the RHI to induce a drop in limb temperature in testosterone-treated individuals, as it did in the placebo group, has to do with testosterone's ability to keep pro-inflammatory cytokines in check, generating less ambiguity in self-detection, peripherally. Homeostatic dysregulation in the RHI may be likened to an autoimmune response, supposedly directed by top-down beliefs about the self.

But how might the “body matrix” (Moseley et al., 2012; Riva, 2017) actually control the immune system? There is data to suggest that inflammation results in increased activation in the insula (Hannestad et al., 2012). Possibly then, this relationship might also work the other way: changes in the insula related to alternations in bodily consciousness might influence cytokine activity. When a region of space occupying a body part is no longer represented as “me”, immune mechanisms in that region may become activated to redirect homeostatic functions. Prior research suggests that prefrontal and insula regions might modulate immune functions via efferent vagus nerve signalling (Pavlov & Tracey, 2005; Thayer, 2009). A mechanism involving the insula is conceivable based on a second body of evidence related to auto-immunity: that pro-inflammatory cytokines are elevated in people with somatoform disorders and alexithymia (Pedrosa et al., 2007), and that they increase in response to social stress (Powell et al., 2013; Quan et al., 2001) and social rejection (Slavich et al., 2012; Dickerson, Gruenewald & Kemeny, 2004), which are both states known to activate the insula (Eisenberger, 2008; Etkin & Wager, 2011; Kross et al., 2011). Cytokines have also been shown, repeatedly, to be elevated in depression (Raison, Capuron & Miller, 2006), a mood disorder whose aetiology is closely linked to social defeat (Becker et al., 2008; Keeney &

Hogg, 1999) and aberrations in insula functioning (Liu et al., 2010; Wiebking et al. 2010). Increases in cytokine activity under stress in those who lack resilience may promote avoidance behaviour via disembodiment mechanisms to influence power relations. For instance many studies show that chronic social defeat in animal models leads to an increase in the production of proinflammatory cytokines such as interleukin-1 α and 6 (Avitsur et al., 2002; Avitsur et al., 2003; Kinsey et al., 2008). Reducing cytokine content instead promotes resilience to social defeat (Hodes et al., 2014). In humans, increases in tumour necrosis factor- α has been shown to correlate with negative social evaluation (Dickerson et al., 2009). Furthermore, these authors found that being negatively judged by others disabled the regulatory ability of glucocorticoids to shut off the inflammatory response. These findings are complimented by reports from patients receiving cortisone treatment, a well-known suppressor of inflammation, who often exhibit mild euphoria and hyperactivity (Warrington & Bostwick, 2006). In studies of social ostracism, most intriguingly, interleukin-6 has been related to activity in mentalising regions of the brain, such as the anterior cingulate (Eisenberger, Inagaki, Rameson, Mashal et al., 2009), which is often recruited for processing the mental states of others (Frith & Frith, 1999) – an advantageous skill when trying to affiliate or appease. Understanding others at the level of the third-person perspective might involve, quite literally, a release from one’s own body, a process enabled to some degree by elevated “not-me” signalling in the body, sustained by the immune system. Eisenberger and Cole (2012) have proposed that threats to the social self² may recruit the same physiological and neural ‘alarm system’ that responds to basic threats to physical integrity.

How does the autoimmune account of disembodiment align with models of predictive coding? Perhaps it is the case that pro-inflammatory cytokines influence precision of interoceptive prediction errors? “Placement” of the body matrix in space might “move” in a similar way that action occurs – via the testing of proprioceptive predictions. Though for homeostatic investment, the predictions may relate more closely to the interoceptive domain. In this model, low precision is likely to enable shifts in homeostatic regulation that deviate from the physical body. This will be an exciting avenue for future research.

² This leads to the intriguing idea that the primary caregiver is embodied as the immune system – the caregiver, the protector of the infant body, becomes internalized as the individual’s own immune response. Some studies do show a link between early childhood abuse and vulnerability to autoimmune disorders (Dallam, 2005; Dube et al., 2012), suggesting that impoverished early care may translate into an immune system that continues to attack the self.

Does the autoimmune theory of testosterone and embodiment cohere with findings from experiments one to three? Harrison et al. (2009) showed that increased circulating interleukin-6 competes for processing within the insula cortex, leading to greater neural recruitment required to successfully perform tasks of cognitive control. We might expect then, that an overall reduction in inflammation, presumably mediated by testosterone (Corcoran et al., 2010; D'Agostino et al., 1999; Hatakeyama et al., 2002; Kanda, Tsuchida & Tamaki, 1996; Maggio et al., 2006; Malkin et al., 2004; Olsen & Kovacs, 1995; Traish, Saad & Guay, 2009; Yesilova et al., 2000), may enable enhanced acuity in interoceptive awareness. IAcc is also known to be impoverished in people who suffer from autoimmune disorders, such as fibromalgia (Duschek, Montoro & Reyes del Paso, 2017), as well as conditions related to increased inflammation, including obesity (Herbert & Pollatos, 2014) and depression (Furman et al., 2013). Furthermore, Ferri et al. (2013), have shown that interoceptive acuity can shape social behaviour by influencing vagal tone, a primary pathway via which the immune response appears to be regulated (Goehler et al., 2000). With regard to temperature changes in the RHI, research has shown that the cytokines, interleukin 1 and 6 function as pyrogens and rising core body temperatures have been linked to cooling of the extremities (Leon, 2002). Lower cytokine content may thus impede processes that regulate body temperature in this way. Finally, literature on a possible role for autoimmunity in the sense of agency does not appear to exist yet, however, given the important role that mood may play in the SoA (Gentsch & Synofzik, 2014), it seems feasible that the strong depression-inducing influences of cytokines may have down-stream effects on agency attributions. A novel line of future research will be to explore whether body ownership, IAcc and the SoA are related to direct measures of peripheral inflammation.

5.5 Implications for current theory

Findings from this thesis have contributed to existing knowledge in the following ways:

This thesis is among the first to explore the effects of testosterone within an embodied cognition framework. Though the picture is far from clear, findings indicate that testosterone modulates the way the body is experienced and represented. These findings have drawn attention to the important role of emotional factors and associated neurochemistries in bodily representation. Specifically, study 2 has shown that the inconsistency in reports of

temperature changes within the RHI (de Haan et al., 2017) may be explained by failure to control for mediating affective variables. For example, de Haan et al. (2017) have suggested that temperature changes might be linked to affective touch. Without including emotion variables, the field will be hampered by purely cognitive models of how the brain constructs a sense of embodiment. Within the field of social endocrinology, a great proportion of the research on testosterone's role in social emotion falls within the cognitive-behavioural paradigm (Burnham, 2007; Mehta & Josephs, 2006; Radke et al., 2015; van Honk et al., 2007). This body of work has revealed key insights into how testosterone regulates social behaviour. However, like research into empathy, which has benefited enormously from the discovery of mirror neurons (Fadiga, Craighero & Olivier, 2005; Gallese et al., 1996; Rizzolatti et al., 1999), our understanding of how competition and social power is regulated within the brain will be equally enhanced by a better appreciation of embodied mechanisms.

As a start, this thesis has pointed to some possible mechanisms. The “approach” orientation characteristic of people with high testosterone and power (Eisenegger et al., 2015; Terburg & van Honk, 2013) may emerge from integrity within sensorimotor systems that support action, both at the level of conveying visceral needs which spur on action, but also in terms of physiological regulation and processes that are involved in the awareness and prediction of action. What it means to be and feel powerful may stem from those bodily signs which signal the readiness and potential to act. Secondly, loss of bodily consciousness may be alarming and serve social needs in much the same way as the processing of biological loss in regulating allostasis. This information may provide the impetus behind defensiveness, particularly under conditions where bodily representations don't easily take account of the *other*. For example, those instead who go the extra mile in the service of others' needs have been found to exhibit larger self-other overlap (Brethel-Haurwitz et al., 2017). Other authors have suggested even that some degree of disembodiment is a normal phenomenon of adopting another's visual-spatial perspective (Kessler & Braithwaite, 2016). Findings from this thesis seem to suggest that testosterone enables self-distinction and the regulation of the physical self. These insights in turn suggest that being powerful is closely tied to the regulation of the self. Radical embodied theories (Kiverstein & Miller, 2015) might argue that regulation of this kind may prevail even at the most rudimentary of levels.

The work presented here has contributed to the growing literature indicating that psychological resilience relates in important ways to the body (Dunn et al., 2010; Haas et

al., 2016; Hodes et al., 2014; Kállai et al., 2015; Moeini-Jazani et al., 2017; Obhi et al., 2012; Werner et al., 2009). That is, the ability to own, represent and control one's own physical body. Testosterone is strongly linked to positive mood states and power in the social sphere (Mazur & Booth, 1998; Ronay & von Hippel, 2010; Wang et al., 1996) and some of this capacity may derive from embodied mechanisms. Incorporating knowledge about embodiment into applied settings should therefore be considered, especially for therapies related to social anxiety and depression.

Finally, the findings presented here raise questions that may be accounted for by drawing on theories of Bayesian predictive coding (Friston, 2010). It has been suggested, for instance, that superior performance on the heartbeat tracking task can be explained by high precision of interoceptive prediction (Ainley et al., 2016). The updating and formulation of generative models may be of particular significance in the study of testosterone, given the importance of predictive coding for contemporary models of brain function (Clark, 2015; Friston, 2009). For instance, Cortlett et al. (2011) propose that behavioural disengagement and withdrawal, at the very opposite end of a spectrum of social power, may occur when no viable predictions can be made or maintained. Furthermore, defensive responding ("jumping to negative conclusions"), for example, may be explained in terms of precision and the process of making decisions in ambiguous contexts (Rubio et al., 2011). If testosterone has a role to play, a research program will be needed to determine exactly how this might occur and under what circumstances, since evidence from experiment one suggests that testosterone may enable adaptive cycling between perceptual and active inference.

5.6 Limitations

Throughout this thesis, inferences have been made about the effects of testosterone on specific embodiment processes, however, in most cases, these processes have been measured indirectly. Interoceptive accuracy was measured via a heartbeat tracking task. This Mental Tracking Method (Schandry, 1981) has received criticism because it is believed that participants sometimes base their estimates on seconds and not actual felt beats (Dunn et al., 2010; Ring & Brener, 1996). If a participant makes an estimate based on seconds and their hear rate happens to be slow, at around 60bpm, this means that they are likely to be more accurate. Although we did not explore this possible confound by assessing participants' sense of time, since the placebo and testosterone group did not differ in terms of heart rate,

and we could assume that those who guess would be distributed across the groups given randomisation, the fact that a difference in accuracy was observed between the groups suggests that guessing based on seconds was not likely to have been a major confound. However, a replication study that employs a within-subjects, pre/post-test design with added assessments to control for time estimation is advisable for future investigations on the effects of testosterone administration on IAcc. The findings presented here should therefore be regarded as preliminary.

Another concern is that generalization of accuracy in the heartbeat tracking method to other domains of interoception has not been firmly established. Some studies have found a positive correlation between heartbeat measures and visceral sensation (Herbert, et al., 2012; Whitehead & Drescher, 1980), but Garfinkel et al. (2017) recently found that while cardiac and gastric acuity were associated, these appeared to be dissociable from touch acuity. Accuracy in perception may diverge across interoceptive axes and the findings presented here should therefore be interpreted in relation to the cardiovascular system. Whether testosterone has any effect on other domains of interoception remains to be seen and should be studied in future research.

The sense of agency (SoA) was measured using the intentional binding paradigm, which is based on Libet's (1983) seminal finding that subjects perceive an intention to act about 200ms prior to actual movement. The finding of enhanced action binding by testosterone administration was taken to imply that the hormone is able to increase the SoA. While intentional binding has been validated by clinical (Edwards et al., 2011; Rowe & Wolpe, 2015) and imaging studies (Lau et al., 2004), Ainley (2015) recently found that action binding did not associate with the amplitude of readiness potential nor with sensory attenuation, a commonly used method for assessing SoA (Wolpe & Rowe, 2014). Moreover, while we were able to control for individual differences in time perception, a potential confound is the reliability of retrospective judgments of time and a participant's ability to use their own actions as markers of time. Similar criticisms have been put forward by Hughes et al. (2013). It is possible therefore that action binding relates to processes underlying the SoA, but is not a true proxy. Exactly how sensorimotor agency relates to feelings of higher-order control is another avenue requiring further investigation, given that here action binding did not associate with positive affective forecasts. It will be important for future studies of

the effects of testosterone on the SoA to triangulate methods, and include assessments of metacognitive judgements.

Homeostatic dysregulation was inferred on the basis of temperature drops in the Rubber Hand Illusion and many of the arguments in this discussion have been premised on this link. It is possible however that thermal changes do not reflect homeostatic imbalances, but instead are a consequence of attention drawn away from the own limb and toward the rubber hand because of the peculiarity of the experience. To the contrary, since testosterone tends to promote vigilance to threatening social cues (Goetz et al., 2014; Terburg et al., 2011), implying a shift in attention *toward* the rubber limb, it is unlikely that attention explains a drop in temperature in response to the illusion since this group displayed no decline. Nevertheless, given the weight of discussion surrounding the potentially disempowering implications of disembodiment, it will be crucial for future studies to assess other parameters of homeostatic dysregulation in bodily illusions, such as inflammatory responses, motor evoked potentials, and the consequences for successful, immediate goal-achievement. This should be assessed in the RHI but also other forms of bodily illusions such as the full body illusion (Salomon et al., 2013) and the enfacement illusion (Tsakiris, 2008).

More generally, a number of limitations are noteworthy. Although in keeping with existing literature (Enter, Spinhoven & Roelofs, 2014; Hermans et al., 2006; van Honk et al., 2011), the sample sizes here were modest and replication studies will be important to validate the current findings. It will be particularly important to establish whether or not the same effects manifest in men, or whether the findings here relate specifically to women (Kivlighan, Granger & Booth, 2005; Thompson et al., 2006), despite homogeneity in many of the ways that testosterone influences the brain and behaviour (van Honk, Bos & Terburg, 2014). For example, there are those who believe that estradiol instead of testosterone may be more relevant for power dynamics in women (Stanton & Schultheiss, 2007) – though, testosterone is known to aromatise to estradiol (Naftolin, Ryan, & Petro, 1971).

The population used in these studies is also somewhat unique, given South Africa's turbulent social history of racial discrimination and violence (Terreblanche, 2002). The focus on bodies in this research may therefore have introduced confound that was not appropriately controlled for and which might be less evident in other populations (see, for example, Durlik and Tsakiris (2014) who report a drop in IAcc following Cyberball rejection in a healthy UK

sample). This concern is compounded by the fact that research does show differences in bodily consciousness between Western and non-Western cultures (Ma-Kellams, 2014). Larger sample sizes controlling specifically for cultural variables as well as replication studies using foreign samples will be able to address these concerns.

Another potential confound in this type of research is that many people have strong folk ideas about the effects of testosterone and one study has shown that these sometimes exert effects on behaviour. Eisenegger et al. (2010) observed that participants who believed they had received testosterone and not placebo, regardless of the double-blind procedure, acted more unfairly in economic games. Such an effect may have less relevance to the current research since our measures did not require social decision-making. Nonetheless, changes in interoceptive acuity might enhance this bias and may have influenced responding on the emotion scales, such as the post Cyberball questionnaire and the Profile of Mood States. What's more is that testosterone levels are also affected by certain forms of activity, such as rigorous exercise or sexual interaction (Dabbs & Mohammed, 1992; van Anders et al., 2007), and even though participants were instructed to avoid these types of activity, because they did not remain at the laboratory during the interval between administration and testing, it is possible that they did not stick to protocol, even though they were asked to report any such incidences. As mentioned in each experimental chapter, levels of circulating testosterone should be assessed. However, it will also be important for future studies to manipulate power behaviourally, using various power induction paradigms (Moeini-Jazani et al., 2017; Obhi et al., 2012).

Finally, many of the ideas put forward throughout this dissertation have been speculative and based on only a few key findings. Embodiment involves a very complex network of brain/body systems and this thesis only managed to scratch the surface. Much of the 'work' presented here has therefore been in the establishment of potential connections between disparate fields and less of a purely empirical nature. Though limitations abound, these limitations pave the way for future research.

5.7 Conclusion

This thesis investigated the effects of testosterone on three well described embodiment processes in women. Though the mechanisms remain unknown, findings show that

testosterone is able to modulate interoceptive accuracy, providing an advantage to acuity in neutral settings which appears to be lost under conditions of social ostracism. Secondly, findings from experiment two suggest that testosterone contributes toward the physiological regulation of the body in response to multisensory manipulation. Finally, this research indicates that testosterone increases the experience of sensorimotor control. These results show that the experience and representation of the body may constitute one channel via which testosterone exerts its gainful effects on social power. This work has contributed to our theoretical understanding of power and suggests that the motivational impetus for social status might be rooted, from an embodied cognition perspective, in an implicit imperative to maintain control of the physical body.

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Appendix 1. Consent form

PARTICIPANT INFORMATION LEAFLET AND INFORMED CONSENT

Informed Consent Document

Instructions:

Please read through the following questions and their answers very carefully. After you have read through the document, please comment on whether you understood everything written in it, and sign where indicated.

If you have any further questions or concerns, please feel free to contact us:

Principal Investigator: Mark Solms

**Department of Psychology
University of Cape Town, Upper Campus
Rondebosch, Cape Town**

Tel: 021 650-3417

Why is this research being done – what is it trying to find out?

This research is being done to find out more about how certain emotions influence perceptions of the body.

Why are you being invited to take part?

You are being invited to take part because you have expressed an interest to participate.

What procedures or other treatments are involved in this research?

During this experiment you will be requested to fill in several questionnaires that will ask you about aspects of your personality and emotional feelings. We will then assess your ability to *keep track of your heart rate / reaction to a human prosthesis / keep track of time in a computer game*³, followed by a memory-recall exercise. Finally, we will take measurements of your height and weight.

What are the risks and discomforts of taking part in this research?

There are no risks involved in this study. All information you provide is kept strictly confidential. Your identity will remain anonymous throughout the research.

Are there any benefits to you if you take part in this research?

You will receive monetary reimbursement.

What happens if you do not want to take part in this research?

Nothing. It is your right to not take part in the research, or to withdraw at any time during the research with no consequence to you, whatsoever. Furthermore you may request that your data be removed confidentially from the dataset.

What happens at the end of this research?

Debriefing will take place once all data is collected. This will allow you the opportunity to learn more about the aims and objectives of the study.

Having read through all the questions and answers, please comment on whether you understand everything written in it, if not then please comment on what you did not understand, or any concerns that you might have:

³ This form has been adapted for display here. Participant forms referred only to the relevant experimental task.

Full names and surname (Please Print): _____

Signature: _____

Date: _____

What if Something Goes Wrong?

Prof. Mark Solms, is covered under University of Cape Town no fault clause of the University of Cape Town Insurance. As per this: the University of Cape Town (UCT) undertakes that in the event of you suffering any significant deterioration in health or well-being, or from any unexpected sensitivity or toxicity, that is caused by your participation in the study, it will provide immediate medical care. UCT has appropriate insurance cover to provide prompt payment of compensation for any trial-related injury according to the guidelines outlined by the Association of the British Pharmaceutical Industry, ABPI 1991. Broadly-speaking, the ABPI guidelines recommend that the insured company (UCT), without legal commitment, should compensate you without you having to prove that UCT is at fault. An injury is considered trial-related if, and to the extent that, it is caused by study activities. You must notify the study doctor immediately of any side effects and/or injuries during the trial, whether they are research-related or other related complications.

UCT reserves the right not to provide compensation if, and to the extent that, your injury came about because you chose not to follow the instructions that you were given while you were taking part in the study. Your right in law to claim compensation for injury where you prove negligence is not affected. Copies of these guidelines are available on request.

What if you have complaints about the study? If you want any information regarding your rights as a research participant, or have complaints regarding this research, you may contact Prof. Marc Blockman, the **Chairperson of the Research Ethics Committee** at the University of Cape Town. The contact information for the HREC is as follows:

Human Research Ethics Committee
Faculty of Health Science
E-52-54 Groote Schuur Hospital Old Main Building
Observatory 7925
Tel: (021) 406 6626
Fax: (021) 406 6411
Email: lamees.emjedi@uct.ac.za

After you have consulted your doctor or the ethics committee and they have not provided you with answers to your satisfaction, you should write to: The Registrar, South African Medicines Control Council (MCC), Department of Health, Private Bag X 828, PRETORIA 0001.

Appendix 2

Statement of permission to include a published work in this thesis

I confirm that I have been granted permission by the University of Cape Town's Doctoral Degrees Board to include the following publication(s) in my PhD thesis, and where co-authorships are involved, my co-authors have agreed that I may include the publication(s):

van der Westhuizen, D., Moore, J., Solms, M., & van Honk, J. (2017).
Testosterone facilitates the sense of agency. *Consciousness and Cognition*,
56, 58-67.

STUDENT NAME: Donné Minné née van der Westhuizen

STUDENT NUMBER: VWSDON002

SIGNATURE:

DATE: 18 February 2018